Entomologia Experimentalis et Applicata

ORIGINAL ARTICLE

Role of herbivore-induced maize volatiles in the chemotactic behaviour of *Telenomus podisi* and *Diceraeus melacanthus*

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Abstract

Plants respond indirectly to herbivore injury in a species-specific way and emit a specific blend of volatiles that are attractive to the enemies of herbivores. We evaluated whether maize plants, *Zea mays* L. (Poaceae), can recognize herbivory damage from a generalist stink bug, *Diceraeus melacanthus* Dallas (Hemiptera: Pentatomidae). This species is not a common pest in maize, but is currently found on maize crops in Brazil. We aimed to answer the following questions: (1) does *D. melacanthus* use maize plant volatiles for host location? (2) Do maize plant chemical volatile profiles change due to feeding by *D. melacanthus*? And (3) do herbivore-induced plant volatiles (HIPVs) emitted by maize plants play a role in the foraging behaviour of the generalist stink bug egg parasitoid *Telenomus podisi* Ashmead (Hymenoptera: Scelionidae)? The results show that females of *D. melacanthus* do not use constitutive volatiles or HIPVs as host location cues. However, feeding by *D. melacanthus* activates maize indirect defence, inducing emission of HIPVs and attracting the herbivore's enemy. Thus, strengthening indirect defence of plants can be a strategy to protect crops in the field by recruiting natural enemies through chemical information, as an additional approach to control *D. melacanthus* within an integrated pest management program.

KEYWORDS

egg parasitoid, Hemiptera, herbivore recognition, HIPVs, Hymenoptera, indirect defence, maize pest, natural enemy attraction, Pentatomidae, Scelionidae, *Zea mays*

INTRODUCTION

Plants are subject to various biotic and abiotic stresses that negatively affect their fitness. To cope with these stresses, plants have evolved sophisticated defence systems (Ogran et al., 2019) that involve constitutive defences, which are continuously expressed, and induced defences, which are triggered by stress conditions (War et al., 2012; Heil, 2014). Inducible defence is thought to have evolved to reduce the energetic costs in response to herbivore feeding or oviposition. Several studies have shown that constantly maintaining high levels of defence can increase a plant's susceptibility to specialist herbivores. Furthermore, the variability in time of induced defence can be used to avoid generalist herbivores that have evolved traits that work against the plant defence (Agrawal & Karban, 1999; Garcia et al., 2021). However, the inducible defence can become disadvantageous if plants are constantly attacked by herbivores. In this case, they should present a higher level of constitutive defence. These defence strategies can act directly on herbivores, or indirectly, by attracting their natural enemies (Dicke, 1999; Cortesero et al., 2000; Agrawal & Karban, 1999).

Injury by herbivores through feeding or oviposition activates plant indirect defence, consisting the emission

of a specific blend of volatiles that may be used by natural enemies as cues to locate their hosts or prey (Turlings et al., 1990; Vet & Dicke, 1992; Dicke, 1999; Colazza et al., 2004; Michereff et al., 2011). In general, herbivore-induced plant volatiles (HIPVs) or oviposition-induced plant volatiles (OIPVs) are used by natural enemies as long-range cues to locate a host (Kessler & Baldwin, 2002). For short-range cues, when parasitoids are close to a host, they may use other chemical cues, such as defensive compounds, sex pheromones, or cuticular hydrocarbons emitted by their hosts (Borges & Blassioli-Moraes, 2017).

Soybean plants, *Glycine max* (L.) Merr. (Fabaceae), that have been damaged by feeding or oviposition by *Euschistus heros* Fabricius release a specific blend of volatiles that are attractive to the egg parasitoid *Telenomus podisi* Ashmead (Hymenoptera: Scelionidae) (Moraes et al., 2005; Michereff et al., 2011). Furthermore, rice plants (*Oryza* spp.) emit HIPVs and attract *T. podisi* when subjected to herbivory by two stink bugs, *Tibraca limbativentris* Stål and *Glyphepomis spinosa* Campos & Grazia (Melo-Machado et al., 2014; Ulhoa et al., 2020).

Maize, *Zea mays* L. (Poaceae), is an important crop for several countries with low incomes, including Brazil, but the growers must cope with a complex of herbivores that use it as food and shelter. The first observation of the stink bug *Diceraeus melacanthus* Dallas (Hemiptera: Pentatomidae) on maize occurred in 1993 (Àvila & Panizzi, 1995), and in the last 10 years, its presence has been more constant, along with other stink bugs such as *E. heros* (Bueno et al., 2015). Attacks by stink bugs (mainly *D. melacanthus* and *E. heros*) on maize crops have intensified due to non-tillage systems (Corrêa-Ferreira & Sosa-Gómez, 2017). In non-tillage systems in Brazil, it is common to grow soybean as the first and maize as the second crop. Stink bugs are a common pest of soybean (Corrêa-Ferreira & Panizzi, 1999; Panizzi et al., 2000; Borges et al., 2011; Depiere & Panizzi, 2011; Corrêa-Ferreira & Sosa-Gómez, 2017), and after it is harvested, the stink bugs remain in the rest of the crop. When the second crop starts to germinate, the stink bugs move to it and feed.

The production losses due to the damage caused by *D. melacanthus* feeding on maize can reach up to 30% (Bianco, 2004; Cruz et al., 2016; Bueno et al., 2021; Da Silva et al., 2021). Nowadays, pesticide application (mainly neonicotinoids) is the only method used for controlling stink bugs in arable crops. Therefore, it is necessary to develop a more sustainable control method to manage them in maize crop systems. The recruitment of natural enemies through sentinel and smart plants is a promising alternative integrated pest management (IPM) strategy (Birkett & Pickett, 2014; Pickett & Khan, 2016; Michereff et al., 2021). Sentinel and smart plants are cultivars and modified plants with traits that allow them to respond earlier to stress and then signal neighbouring plants regarding imminent danger (Pickett & Khan, 2016). For example, sentinel or smart plants experiencing herbivory can emit a blend of volatiles that are attractive to the herbivore's enemies and/or signal neighbouring plants about imminent danger.

The indigenous egg parasitoid *T. podisi* presents high potential for parasitism of various species of stink bugs (including *D. melacanthus*) in crop areas in Brazil (50–80% of eggs are parasitized in field conditions) (Corrêa-Ferreira & Moscardi, 1995; Corrêa-Ferreira & Pacheco, 2000; Sujii et al., 2002; Laumann et al., 2010; Corrêa-Ferreira & Sosa-Gómez, 2017; Queiroz et al., 2018). There is limited information on whether constitutive maize volatiles influence host location by *D. melacanthus* and whether its feeding induces HIPV emission from maize plants. Therefore, an experiment was designed to determine whether (1) the stink bug *D. melacanthus* uses constitutive maize volatiles for host plant location; (2) maize plants injured by *D. melacanthus* emit HIPVs; and (3) *D. melacanthus*-induced HIPVs play a role in the foraging behaviour of the egg parasitoid *T. podisi*.

MATERIALS AND METHODS

Insects

The stink bug *D. melacanthus* and the egg parasitoid *T. podisi* were maintained in separate rooms under controlled conditions [$27 \pm 1\,°C$, $65 \pm 10\%$ r.h., and L14:D10 photoperiod (light: 06:00–20:00 hours)] at Embrapa Genetic Resources and Biotechnology, Brasilia, Brazil (41°43'51.4"S, 47°54'10.5"W). A colony of *D. melacanthus* was established from insects collected in the field from soybean plants in the city of Londrina, Brazil (23°19'11"S, −51°18'46"W). The stink bug was reared in 8-l plastic containers on a diet of soybeans (cv. BRS 247), sunflower seeds (*Helianthus annus* L., Asteraceae), raw peanuts (*Arachis hypogaea* L., Fabaceae), and fresh green beans (*Phaseolus vulgaris* L., Fabaceae). Soybean seeds were cultivated at Embrapa without insecticides, and all other seeds were acquired from an organic market in Brasilia, Brazil, directly from growers. Water was provided in a plastic cup, closed using a lid with a hole that was filled with a small piece of cotton (Borges et al., 2006). Food was supplied twice a week. Clean cotton padding was placed inside the enclosures to provide an oviposition substrate and shelter.

Telenomus podisi was obtained from a laboratory colony raised on *E. heros* eggs. The wasps were maintained in acrylic enclosures (25-cm^2 tissue-culture flasks, angled neck; ICN Biomedicals, Irvine, CA, USA) on eggs of the stink bug *E. heros* (<24 h old) obtained from a colony that was maintained using the same procedure and diet as described above for *D. melacanthus*. Twice a week, adult wasps were fed with a drop of honey (Korin, Brasilia, Brazil). Once the parasitoids hatched from the eggs, they were kept for 24 h in acrylic enclosures for mating, without host eggs. Two-day-old mated naïve females were used in the experiments.

Plants

Maize seeds (cv. Sintético Spodoptera) were obtained from Embrapa Maize and Sorghum in Sete Lagoas, Brazil

(19°27'57"S, 44°14'48"W), and germinated on damp paper. After 3 days, they were transplanted into 250-ml pots filled with a mixture of soil and organic substrate at a proportion of 1:1 wt/wt (Carolina soil, Pardinho, Brazil). They were maintained in a greenhouse with a natural photoperiod and temperature (approximately L14:D10 photoperiod and 19–30 °C temperature range). Plants were watered 4× per week.

The plants used in all experiments had three fully expanded leaves (ca. 12 days old). To obtain plants with herbivory damage (HD), maize plants were infested with adult females of *D. melacanthus* for 10 days after the final moult (two insects per plant). To prevent the insects from escaping, the plants were wrapped in micro-perforated polyethylene plastic bags until they were used in the experiments. To avoid possible chemical signalling between plants, undamaged (UD) maize plants and HD plants were kept in separate rooms under the same environmental conditions (26 ± 1 °C, 65 ± 10% r.h., and L14:D10 photoperiod).

General procedure for Y-tube olfactometer bioassays

Behavioural assays were performed using Y-tube olfactometry (Figure S1), to determine the responses to maize constitutive volatile organic compounds (VOCs) and HIPVs of unmated 8- to 10-day-old *D. melacanthus* females and mated 2-day-old *T. podisi* females. The olfactometers consisted of square acrylic blocks with a Y-shaped cavity compressed between two glass plates (Figure S1). For *T. podisi* bioassays, the blocks were 19 × 19 cm, and the cavity was 1.0 cm thick and 1.5 cm wide, with an 8-cm-long central body, and 7-cm-long arms with an angle of 80° in between (Moraes et al., 2008). For *D. melacanthus* bioassays, the blocks were 23 × 26 cm, and the cavity was 2.0 cm thick and 2.8 cm wide, with a 9-cm-long central body, and 10-cm-long arms with an angle of 80° in between (Moraes et al., 2008).

Humidified and charcoal-filtered air was pushed into the system at a rate of 0.6 L per min (0.3 L per min per arm) and removed at 0.6 L per min. The air was transported through 3.2-l glass chambers and to the olfactometer through silicone tubes. Undamaged and damaged maize plants were placed into these glass chambers as odour sources in the experiments.

Immediately before the bioassays, the stink bugs were removed from the plants. The insects' first choice was assessed as the olfactometer arm that the insect entered first (if it remained there for at least 30 s), and residence time was assessed as the total time that the insect remained in each arm during the bioassays. A single female of *T. podisi* or *D. melacanthus* was introduced at the base of the Y-tube and observed for 10 min. Every five repetitions, a new plant was used, and the positions of the olfactometer arms were changed to avoid bias in insect responses.

Y-tube olfactometer bioassays with *Telenomus podisi* and *Diceraeus melacanthus*

Bioassays with a Y-tube olfactometer were conducted to evaluate whether volatiles emitted by UD and HD maize plants affect the search behaviour of *T. podisi* and *D. melacanthus*. Each female was used only once, and 40 (*T. podisi*) or 30 (*D. melacanthus*) replicates were conducted for each treatment combination: (1) volatiles from UD vs. HD plants at four time intervals after start of the damage (24, 48, 72, and 96 h); (2) air vs. volatiles from HD plants at 24, 48, 72, and 96 h after damage; and (3) air vs. volatiles from UD plants. Bioassays were carried out between 10:00 and 15:00 hours (*T. podisi*) or between 15:00 and 18:00 hours (*D. melacanthus*).

Plant volatile collections

Volatiles from UD and HD plants were collected at 0–24, 24–48, 48–72, and 72–96 h after the infestations were initiated (n = 8 replicates for each time and treatment combination). These intervals were selected based on previous work, which showed that plants start to emit HIPVs after 48 h (rice plants) and 72 h (soybean plants) of herbivory (Michereff et al., 2011; Ulhoa et al., 2020). To determine the chemical profile of volatiles of UD and HD plants, three UD plants or three HD plants were placed in cylindrical 10-l glass chambers. For all treatments, volatiles were collected in glass tubes containing the adsorbent Porapak Q (100 mg, 80–100 mesh) and connected via a PTFE tube to a vacuum pump with a flow of 0.6 L per min.

The air entrance was connected to an airflow filtered with activated charcoal (1.0 L per min), creating a positive push-pull system (Moraes et al., 2008). The trapped volatiles were eluted from the adsorbent every 24 h using 500 μl of *n*-hexane and concentrated to 50 μl under N_2 flow. Extracts were stored at −20 °C until analyses by coupled gas chromatography-flame ionization detector (GC-FID) and coupled GC-mass spectrometry (GC–MS).

Chemical analysis

For qualitative analysis, selected extracts were analysed using GC (GC7890A; Agilent, Santa Clara, CA, USA) coupled with MS (5975MSD; Agilent) equipped with a quadrupole analyser, a non-polar DB-5MS column (30 m × 0.25 mm internal diameter and 0.25 μm film thickness; J&W Scientific, Folsom, CA, USA), and a splitless injector with helium as the carrier gas. Ionization was by electron impact (70 eV and source temperature 200 °C). The temperature program was 50 °C (2 min), 5 °C per min to 180 °C (0.1 min), and 10 °C per min to 250 °C (20 min). Data were collected and analysed with GC–MS CHEMSTATION v.2.1 software (Agilent). Volatile compounds in the extracts were identified by comparing spectra with library databases (NIST 2008, Gaithersburg, MD, USA) or published spectra and confirmed using authentic standards if available.

For quantitative analyses, all extracts were analysed by GC-FID (7890A; Agilent) using a non-polar DB-5MS column (J&W Scientific) and a temperature program as described above. The column effluent was analysed with an FID at 270 °C. One µl of 16-hexadecanolide was added as an internal standard (IS) with a final concentration of $9.8\,\mu g\,ml^{-1}$. The response factor for all compounds was considered 1.0. Two µl of each sample was injected using splitless mode with helium as the carrier gas. The amounts of volatile chemicals released by the plants at all time intervals were calculated in relation to the area of the IS. Data were collected with OPENLAB v.A02.01software (Agilent) and recorded using Excel (Microsoft, Redmond, WA, USA).

Chemicals

n-Hexane (95%; suitable for pesticide residue analysis), Porapak Q, indole (99%), α-camphene (95%), (E)-(1R,9S)-caryophyllene (98%), myrcene (95%), α-humulene (96%), geranylacetone (97%), ocimene (mixture of isomers, >90%), geranyl acetate (97%), and cyclosativene (99%) were purchased from Sigma-Aldrich (Steinheim, Germany). (E)-2-Hexenal (95%) and (Z)-3-hexen-1-ol (98%) were purchased from Sigma-Aldrich (Gillingham, Dorset, UK). (E)-β-Farnesene (98%) was provided by Shin-Etsu (Tokyo, Japan). (Z)-3-Hexenyl acetate (98%) was purchased from Alfa Aesar (Heysham, UK). (E)-2-Hexenyl acetate (97%) and linalool were purchased from TCI America (Portland, OR, USA). (E)-4,8-Dimethyl-1,3,7-nonatriene (DMNT) and (E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT) were synthesized from geraniol and (E,E)-farnesol, respectively (Leopold, 1990).

Statistical analysis

Insect first choices in the Y-tube olfactometer were analysed using logistic regressions to estimate the probability of each choice (Magalhães et al., 2016; Michereff et al., 2019), and the hypotheses of non-preference (50% probability of choosing each treatment) were assessed using the Wald χ^2 test. The residence times in each arm of the olfactometer were subjected to paired t-tests. If the insects did not move after 3 min, they were considered unresponsive and were not included in the statistical analysis.

The total amounts of volatiles and individual compounds in each volatile sample were analysed using generalized linear model (GLM) with a gamma distribution and the inverse link function followed by deviance analysis (ANODEV). If the analyses showed significant effects between treatments, the means were compared using contrast analysis with a 95% confidence level. To assess the influence of the treatments on the compound profile, principal component analysis (PCA) was applied to the four evaluated intervals (0–24, 24–48, 48–72, and 72–96 h) using the variance and covariance matrix in PAST v.3.10 software. All other analyses were performed using R v.2.13.0 (R Core Team, 2009).

RESULTS

Y-tube olfactometer assays with *Telenomus podisi*

In first-choice tests, *T. podisi* females showed a preference for HD plants at 48 h after infestation vs. UD plants ($\chi^2 = 3.48$, P = 0.04), and for HD plants at 48 h ($\chi^2 = 4.68$, P = 0.03) and 72 h ($\chi^2 = 6.03$, P = 0.01, all d.f. = 1) after infestation vs. air. The parasitoid did not discriminate between other treatments (Figure 1A, Table S1). The residence time of *T. podisi* females was longer in the arm containing the volatiles from HD plants at 48 h (t = 4.29, P < 0.001) and 72 h (t = 2.64, P = 0.01, both d.f. = 39) after infestation vs. air. There was no preference for any of the other treatments (Figure 1B, Table S1).
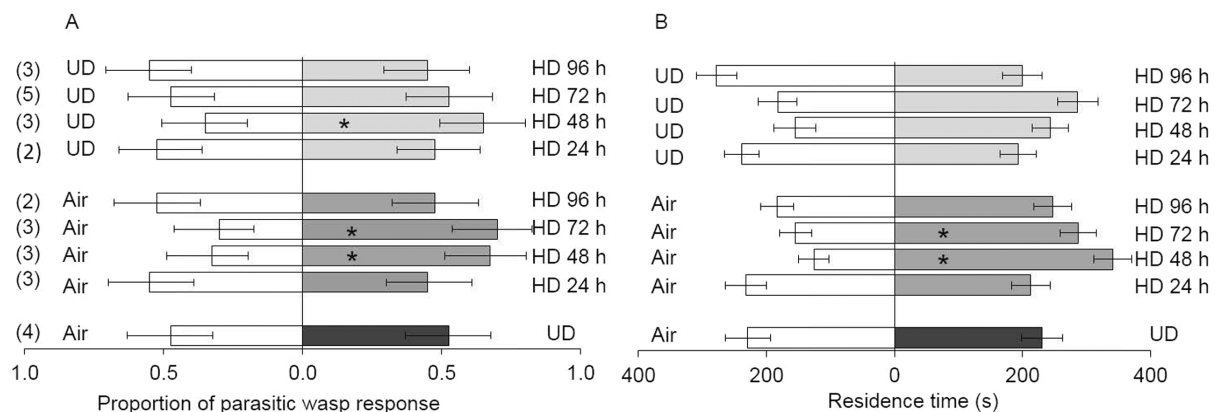

FIGURE 1 (A) Mean (± 95% confidence interval) proportion of first choice and (B) mean (± SD) residence time (s) of females of the egg parasitoid *Telenomus podisi* in a Y-tube olfactometer exposed to volatiles of maize plants, at four time intervals since initiation of herbivory (24–96 h). UD, undamaged; HD, herbivore-damaged (by *Diceraeus melacanthus*); air, control. Numbers in parentheses indicate the wasps that did not respond to any treatments. An asterisk indicates a significant difference between odour sources (A: Wald χ^2 test; B: paired t-test: P < 0.05)
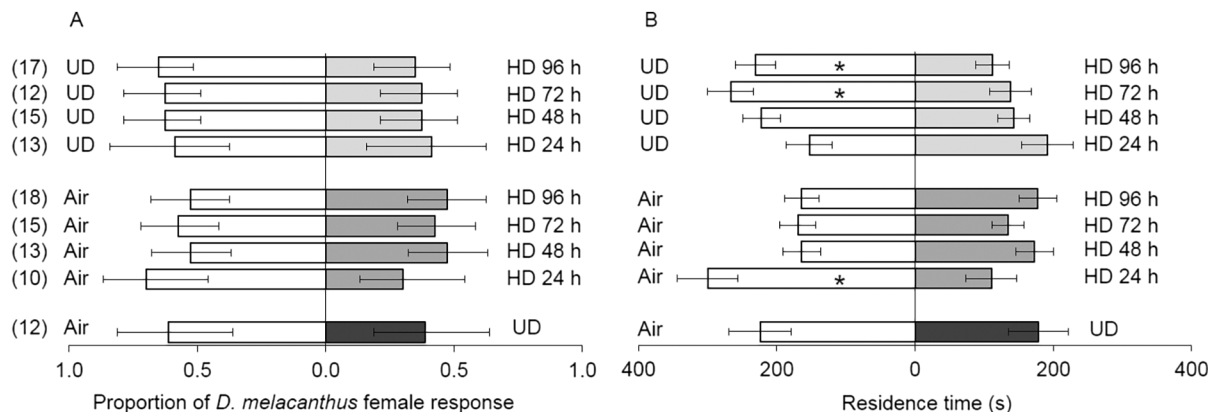
FIGURE 2 (A) Mean (± 95% confidence interval) proportion of first choice and (B) mean (± SD) residence time (s) of females of the stink bug *Diceraeus melacanthus* in a Y-tube olfactometer exposed to volatiles of maize plants, at four time intervals since initiation of herbivory (24–96 h). UD, undamaged; HD, herbivore-damaged (by the stink bug); air, control. Numbers in parentheses indicate the insects that did not respond to any treatments. An asterisk indicates a significant difference between odour sources (A: Wald χ^2 test; B: paired t-test: P < 0.05)
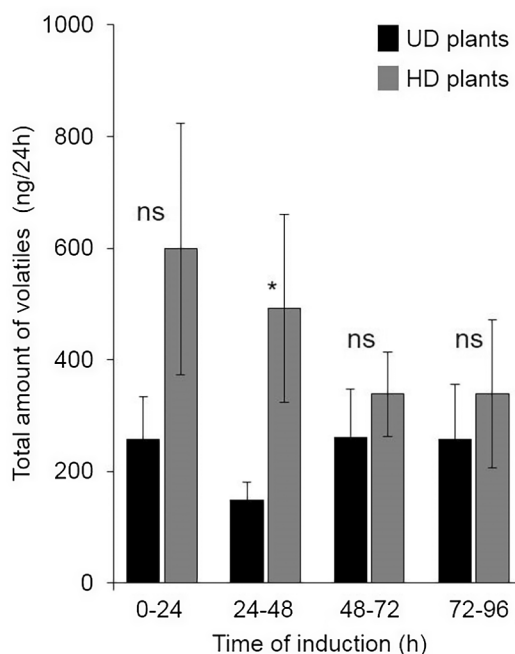

FIGURE 3 Mean (± SEM) total amounts (ng per 24 h) of volatiles emitted by maize plants damaged by the stink bug *Diceraeus melacanthus* (HD) at four-time intervals since initiation of herbivory (24–96 h) and undamaged control plants (UD). The asterisk indicates a significant difference between treatments (contrast analysis: P < 0.05; ns, P > 0.05)

Y-tube olfactometer assays with *Diceraeus melacanthus*

In first-choice tests, *D. melacanthus* females did not show a preference for any of the odour sources offered (Figure 2A, Table S2). However, they spent more time in the arm with volatiles from UD vs. HD plants at 72 h (t = 2.17, P = 0.03) and 96 h (t = 2.47, P = 0.01, both d.f. = 29) after infestation. Likewise, *D. melacanthus* spent more time in the arm with air vs. HD plants

at 24 h after infestation (t = −2.55, d.f. = 29, P = 0.01). There was no preference for any other treatments (Figure 2B, Table S2).

Plant volatile analysis

In HD plants, volatile emission increased at 24–48 h after infestation (χ^2 = 33.73, d.f. = 1, P < 0.001) (Figure 3). At the other time intervals, there was no significant difference between the total amount of volatiles released by HD vs. UD plants (0–24 h: χ^2 = 1.849, P = 0.17; 48–72 h: χ^2 = 0.590, P = 0.44; 72–96 h: χ^2 = 1.730, P = 0.19, all d.f. = 1) (Figure 3). The UD and HD plants emitted similar volatile profiles but with quantitative differences (Table 1). There were no significant differences in the emission of individual compounds at the 0–24 h time interval for UD vs. HD plants (Table 1).

At the 24–48 h time interval, HD plants emitted higher levels of (*Z*)-3-hexenyl acetate (χ^2 = 4.325, P = 0.037), (*RS*)-linalool (χ^2 = 9.371, P = 0.002), methyl salicylate (χ^2 = 5.065, P = 0.024), geranyl acetate (χ^2 = 7.887, P = 0.049), DMNT (χ^2 = 8.073, P = 0.004), cyclosativene (χ^2 = 19.775, P < 0.001), α-humulene (χ^2 = 6.768, P = 0.009), (*E*)-β-caryophyllene (χ^2 = 20.091, P < 0.001), δ-cadinene (χ^2 = 17.234, P < 0.001), and TMTT (χ^2 = 4.650, P = 0.031, all d.f. = 1) compared to UD plants. At 48–72 h, the compounds DMNT (χ^2 = 5.176, P = 0.022) and geranyl acetate (χ^2 = 4.218, P = 0.039) were released in higher amounts by HD plants compared to UD plants, and at 72–96 h, (*E*)-β-caryophyllene (χ^2 = 32.907, P < 0.001) and cyclosativene (χ^2 = 4.397, P = 0.035, all d.f. = 1) were emitted in higher amounts by HD plants compared to UD plants (Table 1, Table S3).

A PCA confirmed the difference in the chemical profile of volatiles released by HD and UD plants at 24–48 h; treatments were grouped based on the emitted VOCs, and all compounds appeared to be related to HD plants. The first two axes explained 70% of the variation (Figure 4B). At 0–24, 48–72, and 72–96 h, there is no clear

TABLE 1 Mean (± SEM) amounts (ng per 24h) of volatiles emitted by maize plants damaged by the stink bug *Diceraeus melacanthus* (HD) or undamaged plants (UD) at four time intervals since initiation of herbivory

Compounds	Retention index	0–24 h		24–48 h		48–72 h		72–96 h	
		UD	HD	UD	HD	UD	HD	UD	HD
β-Myrcene	991	15.23±7.09	50.71±25.24	10.86±2.82	25.72±8.74	19.93±6.63	12.41±1.69	17.10±8.00	10.67±1.65
(Z)-3-Hexenyl acetate	1004	40.47±13.26	77.37±34.35	16.71±2.63a	48.41±21.13b	27.85±12.66	19.32±3.98	32.19±15.85	15.69±4.23
(E)-Ocimene	1050	10.16±5.25	7.40±3.22	2.18±0.89	19.50±18.53	7.06±1.92	14.90±5.92	8.97±1.92	1.79±1.96
(RS)-Linalool	1101	25.07±7.81	66.62±25.49	19.46±2.60a	55.05±21.99b	20.85±6.15	24.86±2.90	31.80±10.00	11.13±5.94
DMNT[1]	1113	7.95±2.94	45.44±23.22	5.14±1.73a	34.72±7.45b	6.91±3.50a	23.99±2.52b	9.17±4.36	13.89±3.11
Methyl salicylate	1200	37.00±12.52	107.79±50.00	18.72±4.65a	46.41±15.75b	32.61±14.22	41.68±6.65	34.16±15.18	24.07±5.16
Indole	1301	11.80±2.46	37.89±15.78	6.14±1.11	21.14±10.06	13.21±5.95	9.42±3.73	16.91±8.04	56.16±28.69
Cyclosativene	1386	42.41±8.18	79.18±24.56	28.25±3.07a	85.69±19.79b	42.17±11.03	80.72±21.09	31.89±8.69a	76.08±26.65b
Geranyl acetate	1389	3.44±1.11	7.91±2.16	5.88±3.42a	11.53±3.59b	4.24±1.28a	9.48±1.74b	4.60±1.03	10.11±2.47
(E)-β-Caryophyllene	1439	7.74±2.78	35.92±11.68	6.29±1.43a	58.26±11.45b	21.36±5.16	45.50±12.84	10.11±3.01a	34.59±11.57b
Geranylacetone	1451	20.74±4.22	28.28±5.74	7.17±2.13	25.09±13.96	20.71±5.97	12.85±4.39	13.68±5.60	32.07±22.83
(E)-β-Farnesene	1456	11.53±4.36	10.74±2.99	9.21±2.05	11.66±2.29	18.08±5.11	8.36±2.14	16.15±8.09	13.54±3.44
α-Humulene	1476	13.60±2.65	22.38±4.66	6.23±1.47a	18.24±6.44b	6.19±1.73	13.13±2.84	15.23±4.93	11.57±3.75
δ-Cadinene	1492	5.01±0.78	7.76±1.95	3.17±0.25a	7.59±1.66b	10.15±2.63	6.62±1.41	5.20±0.98	10.04±2.45
TMTT[2]	1578	5.48±1.51	13.66±4.39	2.98±2.29a	22.57±5.27b	10.15±2.63	15.27±2.06	10.03±2.38	18.15±8.60

UD vs. HD contrasts: all pairs were tested; means within a time-interval followed by different letters are significantly different (contrast analysis: P < 0.05).

[1] (E)-4,8-Dimethyl-1,3,7-nonatriene.

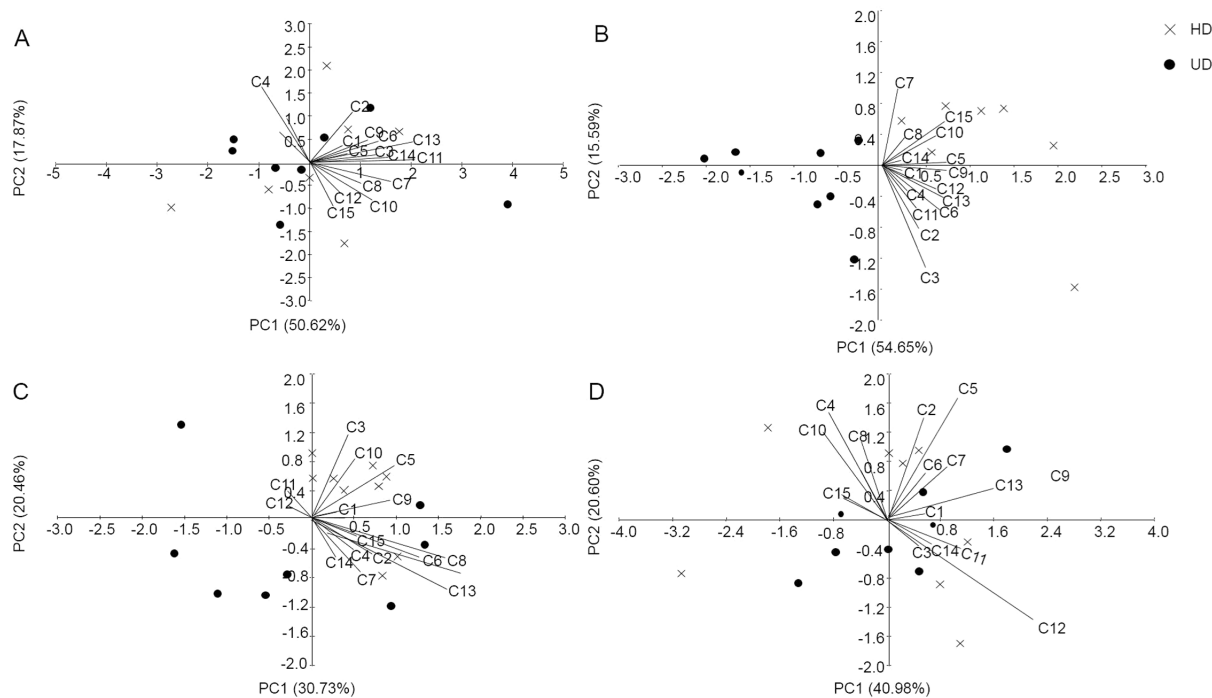[2] (E,E)-4,8,12-Trimethyl-1,3,7,11-tridecatetraene.

FIGURE 4   Principal component analysis (PCA) bi-plots derived from volatiles emitted by maize plants submitted to herbivory by *Diceraeus melacanthus* (HD) and undamaged plants (UD) at four time points after initiation of herbivory: (A) 0–24, (B) 24–48, (C) 48–72, and (D) 72–96 h. C1 = β-myrcene, C2 = (*Z*)-3-hexenyl acetate, C3 = (*E*)-ocimene, C4 = (*RS*)-linalool, C5 = (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT), C6 = methyl salicylate, C7 = cyclosativene, C8 = indole, C9 = geranyl acetate, C10 = (*E*)-β-caryophyllene, C11 = geranylacetone, C12 = (*E*)-β-farnesene, C13 = α-humulene, C14 = δ-cadinene, and C15 = (*E*,*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT).

separation between the two treatments (UD and HD) (Figures 4A, C, D).

DISCUSSION

Diceraeus melacanthus females do not use maize constitutive VOCs or HIPVs as host location cues, as they did not prefer volatiles from UD or HD plants over clean air in the bioassays. In contrast, in maize plants on which *D. melacanthus* fed, indirect defences were activated and HIPVs were released, which attracted the herbivore's enemy, *T. podisi*. Plants are equipped with several mechanisms of defence against herbivores, and the activation of indirect defence appears to be a general plant response occurring in various crop systems infested with chewing or sucking generalist and specialist insects (Ali & Agrawal, 2012; Blassioli-Moraes et al., 2016).

The non-response of *D. melacanthus* to constitutive VOCs was different from what was observed in other stink bugs, such as *E. heros*, *T. limbativentris*, and *Dichelops furcatus* (Fabricius), which are all attracted to constitutive volatiles from their host plants (Michereff et al., 2011; Ulhoa et al., 2020; Jacobi et al., 2021). The observed non-response of *D. melacanthus* may be explained by this stink bug not using maize as a host plant. Stink bugs are key pests of soybean. After harvesting soybeans in a non-tillage system, the insects remain on the rest of the plants, and when maize, as a second crop, is cultivated, the insects move

to this new crop and feed on it (Depiere & Panizzi, 2011). Therefore, they do not need to use semiochemicals from maize plants in the field, as they are already in the area.

The indirect plant response is species-specific, and the same plant damaged by different insect species releases a different blend of volatiles (Dicke, 1999). The results of this study support the notion that HIPV blends are species-specific in terms of not only the quantity released, but also the compound composition. In this study, emissions of 10 VOCs were increased at 24–48 h after herbivore infestation, among which cyclosativene, (*E*)-β-caryophyllene, (*RS*)-linalool, (*Z*)-3-hexenyl acetate, and methyl salicylate. Two previous studies were conducted with the same maize genotype (cv. Sintético Spodoptera) that was injured by second instar *Spodoptera frugiperda* J.E. Smith. The results showed that the major compounds induced by larval herbivory were cyclosativene, (*E*)-β-caryophyllene, (*RS*)-linalool, (*Z*)-3-hexenyl acetate, (*E*)-β-farnesene, δ-cadinene, indole, α-humulene, and TMTT (Michereff et al., 2019, 2021).

Indole, a key compound for plant–plant communication, was not significantly increased with *D. melacanthus* injury, and its increased emission appears to be related to injury from some lepidopteran larvae, such as *Spodoptera littoralis* (Boisduval) and *S. frugiperda* (Erb et al., 2015; Michereff et al., 2019). Interestingly, at the other time points evaluated (0–24, 48–72, and 72–96 h), HD plants emitted higher quantities of certain compounds than UD plants, like cyclosativene, DMNT, geranyl acetate, and (*E*)-β-caryophyllene. However, the egg parasitoid responded only to the more

complex HIPV blend released at 24–48 h after herbivore infestation.

Telenomus podisi is a generalist parasitoid with some preference for parasitizing *E. heros* eggs compared to the eggs of other stink bugs, such as *D. melacanthus* (Laumann et al., 2010). This egg parasitoid responds to HIPVs emitted by various crops in response to feeding by different stink bugs, such as those emitted by soybean plants with feeding injury from *E. heros* (Moraes et al., 2005; Michereff et al., 2011). Other examples are rice plants with feeding injury from *T. limbativentris* (Melo-Machado et al., 2014; Ulhoa et al., 2020) and *G. spinosa* (Ulhoa et al., 2020), as well as sunflower and maize plants fed on by *E. heros* (Dias et al., 2016).

In all these systems, the chemical composition of the plants' emitted volatile blends is different. For example, soybean plants with feeding injury from *E. heros* emit higher amounts of (*E,E*)-α-farnesene, methyl salicylate, (*E*)-2-octenal, (*Z*)-3-hexenyl acetate, and TMTT (Moraes et al., 2005, Michereff et al., 2011). Rice plants with *T. limbativentris* and *G. spinosa* feeding injury emit increased amounts of sesquiterpenes such as α-copaene, α-zingiberene, α-curcumene, β-sesquiphellandrene, β-caryophyllene, and α- and δ-cadinene (Ulhoa et al., 2020), whereas sunflower and maize plants with *E. heros* herbivory show suppressed emission of volatiles (Dias et al., 2016). These studies show the variability of chemical plant volatiles that attract *T. podisi*.

The response of *T. podisi* to all these different blends of plant volatiles can involve recognition of the variation in the total amount of volatiles vs. the plant background, as well as changes in the ratios between specific components (Bruce & Pickett, 2011). An egg parasitoid presenting an innate response to reliable HIPVs has a higher chance of locating its host (Bin et al., 1993; Büchel et al., 2011; Cusumano et al., 2015; Michereff et al., 2016). In addition, Vet & Dicke (1992) proposed that generalist parasitoids are more ready to learn to adapt, which means that *T. podisi* might also have learned to recognize maize HIPVs.

A positive effect of HIPVs on parasitoid densities in crop areas has been observed in multiple studies using synthetic HIPVs (Simpson et al., 2011a, 2011b; Vieira et al., 2014), as well as in studies based on intercropping plants in a push-pull system to protect maize in sub-Saharan Africa (Khan et al., 2014; Pickett et al., 2014; Pickett & Khan, 2016). When using synthetic volatile blends or plants emitting HIPVs in field conditions for biological control, one must consider whether the prey or host is present in the area. If it is not, there can be a negative effect on the natural enemy population; parasitoids and predators may then learn a negative association of HIPVs and the presence of prey or hosts, and the population level of natural enemies may consequently decrease (Simpson et al., 2011a, 2011b; Blassioli-Moraes et al., 2016, 2022; Pickett & Khan, 2016; Venzon et al., 2019). Therefore, the use of HIPVs for crop protection needs to be explored from a broader perspective, with an evaluation of the best time of application. Furthermore, it should be combined with rewards for the natural enemy (Simpson et al., 2011a, 2011b ; Venzon et al., 2019).

The efficiency of HIPVs can be increased by combining them with edible resources, such as plants that can provide pollen and nectar, as well as shelter for eggs. Plants genetically modified (GM) to emit HIPVs can have the same effect as synthetic lures that release HIPVs, i.e., the natural enemies may be attracted, but not find the prey or host. However, GM plants could be designed to activate a stronger and faster indirect defence after an herbivore attack.

In summary, the results of this study show that feeding by *D. melacanthus* **activates maize indirect defence, inducing emission of HIPVs that are attractive to** the herbivore's natural enemy, *T. podisi*. Thus, within an IPM system, recruiting natural enemies through chemical information can be a promising strategy for controlling *D. melacanthus* populations in field conditions. Nevertheless, further studies are necessary to evaluate the efficiency of maize HIPVs in soybean and maize field conditions for stink bug control.

AUTHOR CONTRIBUTIONS

Izabela Nunes do Nascimento: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Mirian Fernandes Furtado Michereff:** Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); writing – review and editing (equal). **Walter Esfrain Pereira:** Conceptualization (equal); writing – review and editing (equal). **Paulino Ribeiro Villas Boas:** Conceptualization (equal); resources (equal); writing – review and editing (equal). **Marcos Rafael Gusmão:** Conceptualization (equal); resources (equal); writing – review and editing (equal). **John Caulfield:** Conceptualization (equal); writing – review and editing (equal). **Raul Laumann:** Conceptualization (equal); writing – review and editing (equal). **Miguel Borges:** Conceptualization (equal); funding acquisition (equal); project administration (equal); writing – review and editing (equal). **Maria Carolina Blassioli-Moraes:** Conceptualization (lead); formal analysis (equal); funding acquisition (lead); investigation (lead); methodology (equal); supervision (lead); writing – original draft (equal); writing – review and editing (equal).

ACKNOWLEDGMENTS

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Redape at doi.org//10.48432/FT5Q7R

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Statistical analysis of first-choice data and residence time of the egg parasitoid *Telenomus podisi* in Y-tube olfactometer bioassays. Odour sources were maize plants with herbivory of *Diceraeus melacanthus* (HD) at four time intervals since the start of herbivory, undamaged maize plants (UD), and clean air (control)

Table S2. Statistical analysis of first-choice data and residence time of *Diceraeus melacanthus* in Y-tube olfactometer. Odour sources were maize plants with herbivory of conspecifics (HD) at four time intervals since the start of herbivory, undamaged maize plants (UD), and clean air (control)

Table S3. Statistical analysis of volatile organic compounds released by maize plants with herbivory of *Dichelops melacanthus* (HD) at four time intervals since the start of herbivory or undamaged maize plants (UD)

Figure S1. (A) Schematic drawing of the Y-olfactometer with plants in glass chambers as odour sources. The arrows indicate the airflow direction. (B) Photograph of the Y-olfactometer setup.