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Volatiles mediate host-selection in the corn hoppers *Dalbulus maidis* (Hemiptera: Cicadellidae) and *Peregrinus maidis* (Hemiptera: Delphacidae)

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Abstract

Volatile organic compounds (VOCs) released by plants are generally involved in host recognition and host selection for many phytophagous insects. However, for leafhoppers and planthoppers, host recognition is mainly thought to involve a phototactic response, but it is not clear if a host plant could be selected based on the volatile cues it emits. In this study we evaluated olfactory responses in dual choice tests of two Hemiptera species, *Dalbulus maidis* (De Long) (Cicadellidae) and *Peregrinus maidis* (Ashmead) (Delphacidae), vectors of maize-stunting diseases, to three maize (*Zea mays* L.) germplasms, a temperate and a tropical hybrid and a landrace. VOCs emitted by the germplasms were collected and identified using gas chromatography-mass spectrometry. The temperate hybrid released significantly more VOCs than the tropical hybrid and the landrace, and its volatile profile was dominated by (±)-linalool. *D. maidis* preferred odours emitted from the temperate hybrid, whereas *P. maidis* preferred odours from the tropical hybrid and the landrace over the temperate one. In order to test if linalool plays a role in the behavioural responses, we assayed this compound in combination with the tropical hybrid, to provide other contextual olfactory cues. *D. maidis* was attracted to the tropical hybrid plus a 0.0001% linalool solution, indicating that this compound could be part of a blend of attractants. Whereas addition of linalool resulted in a slight, though not significant, reduction in host VOC attractiveness for *P. maidis*. Both hopper species responded to olfactory cues in the absence of supplementary visual cues.

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Introduction

Plant productivity is affected by Auchenorrhyncha (Hemiptera) hoppers throughout the world. These species transmit diseases (virus, phytoplasmas, spiroplasmas and bacteria) and also remove sap and debilitate the entire plant (Nault & Rodríguez, 1985). In fact, some of the main maize diseases in subtropical America are caused by maize-stunting pathogens transmitted in a persistent and propagative manner by leafhoppers and planthoppers, such as *Dalbulus maidis* (De Long) (Hemiptera: Cicadellidae) and *Peregrinus maidis* (Ashmead) (Hemiptera: Delphacidae). Despite the economic importance of delphacid and cicadellid vectors and considering that many of them are host-specific herbivores, there has been little attention paid to their olfactory sensitivity, which could be crucial in the development of new strategies for pest management. For leafhoppers and planthoppers, most studies suggest that olfaction is only supplementary to visual cues (Todd *et al.*, 1990; Cook & Denno, 1994; Fereres & Moreno, 2009; La Grange *et al.*, 2017; Zhang *et al.*, 2017), which are unlikely to provide host-specific information (Compton, 2002). However, the role of olfaction in Auchenorrhyncha has not yet been fully clarified since it is known that some leafhoppers and planthoppers respond to olfactory cues in the absence of visual stimuli (Obata *et al.*, 1981; Youn, 2002; La Grange *et al.*, 2017). Also, the phototactic response to plant-reflected wavelengths may be modified by plant volatiles (Fereres & Moreno, 2009).

Dalbulus maidis, a leafhopper, is considered a serious maize pest throughout most of the Americas, from southern USA to northern Argentina, primarily because it is the vector of corn stunt spiroplasma (CSS), maize rayado fino virus and maize bushy stunt mycoplasma (Carloni *et al.*, 2013; Virla *et al.*, 2013). *Dalbulus maidis* is a specialist herbivore feeding only on plants of the genus *Zea*, like maize (*Zea mays* L.) and its wild relatives, the teosintes (*Zea* spp.). In South America, it is the most prevalent leafhopper species associated with maize (Paradell *et al.*, 2001; Luft Albarracin *et al.*, 2008, 2017). CSS, one of the most important stunting diseases in maize, is caused by the mollicute *Spiroplasma kunkelii* (Spiroplasmataceae). The decrease in the yield of plants with CSS can be very high, from 12 to 100%, depending on the severity of symptoms (Virla *et al.*, 2004*a*).

Peregrinus maidis is a broadly distributed planthopper, recognized as a maize pest, vector of other viral diseases, such as Maize Stripe Tenuivirus, Maize Mosaic Rhabdovirus, Maize Iranian Mosaic Virus, Maize Sterile Stunt Virus and also Mal de Río Cuarto Virus (MRCV) (Virla *et al.*, 2004*b*), one of the most prejudicial stunting pathogens in temperate South America (Lenardón *et al.*, 1998; Argüello Caro *et al.*, 2013). MRCV is transmitted by planthoppers (Delphacidae), being *Delphacodes kuscheli* (Fennah) the main vector (Arneodo *et al.*, 2002; Gimenez Pecci *et al.*, 2012). Unlike *Dalbulus* leafhoppers, *P. maidis* apparently adapted to maize as a host in post-Columbian times (Nault, 1983). It is a polyphagous insect, most frequently associated with *Sorghum* spp., but has also been found on *Panicum* spp. and other grasses (Tsai, 1996; Marino de Remes Lenicov & Paradell, 2012; Diaz *et al.*, 2016). Like many other planthoppers, adults have dual wing form, short wing (brachypterous) and long wing (macropterous). Brachypterous are unable to fly and occur when the environmental conditions are suitable for rapid population increase. In contrast, macropterous are produced when the population is too high to be sustained by the host plant, and thus migration to other hosts is favoured (Singh & Seetharama, 2008).

Dalbulus maidis and *P. maidis* often coexist in subtropical maize fields, where two kinds of maize germplasms are cultivated by farmers; temperate germplasms are planted early in spring (off-season), and tropical germplasms are planted afterwards in the summer, soon after temperate maize harvest. Tropical germplasms are generally thought to be more resistant to maize stunting pathogens, because they have been developed from landraces obtained from area with high disease pressure. The coexistence of tropical and temperate maize in the beginning of the summer and the off-season maize harvest generates conditions under which CSS becomes a generalized problem in subtropical areas from South America (Oliveira *et al.*, 2013). Apparently, part of the mechanism of resistance to CSS in maize germplasms involves less settling of the disease vectors (Carpane & Ingrassia, 2012). In a field experiment, Virla *et al.* (2010) demonstrated that Bt maize plots had significantly more *D. maidis* leafhoppers than the corresponding plots with a non-Bt maize isoline. Consequently, the authors observed that Bt maize were more affected by CSS than its non-Bt isoline (Virla unpublished). It is unknown if the preference for a particular germplasm involves phototactic responses, olfactive responses or both, but understanding the mechanism could be very important in the development of resistant hybrids.

Considering that Cicadellidae is a large family with at least 22,000 species (McKamey, 2002), olfaction has been assessed in relatively few species (Saxena & Saxena, 1974; Khan & Saxena, 1985; Todd *et al.*, 1990; Bullas-Appleton *et al.*, 2004; Ranger *et al.*, 2005; Patt & Setamou, 2007; Bento, 2008; Mazzoni *et al.*, 2009; Oluwafemi *et al.*, 2011; La Grange, 2016 and Zhang *et al.*, 2017). In most leafhopper species, including *D. maidis*, the primary effect of host odour seems to be enhancing responsiveness to visual cues. To our knowledge, only two studies have proved that leafhoppers can discriminate between a preferred and non-preferred host species only based on the emitted volatile organic compounds (VOCs); *Empoasca fabae* (Harris) responded to leaf steam distillates of *Medicago sativa* L., discriminating between alfalfa varieties (Ranger *et al.*, 2005) and *Cicadulina storeyi* China discriminated between headspace VOC samples of infested and uninfested maize seedlings (Oluwafemi *et al.*, 2011). In a previous study with *D. maidis*, Todd *et al.* (1990) found that there is an interaction between visual and olfactory stimuli during host finding. A strong orientation response of *D. maidis* towards yellow and green light plus maize volatiles was observed, but they observed no significant differences when a maize extract was assayed alone, without the green light stimulus, vs. a solvent control. Todd *et al.* (1990) also proved that maize volatiles not only have an effect on orientation, but also on postcontact behaviours not associated with feeding.

In planthoppers, olfaction has been even less investigated, and selection of a host was largely thought to involve random settling of macropterous, and host plant specificity resulting because adults accumulate on favourable plants and selectively migrate from unsuitable hosts (Cook & Denno, 1994). Nevertheless, olfaction has been studied in three species (Obata *et al*., 1981, 1983; Liu *et al*., 1994; Youn, 2002; Wang *et al*., 2015). Moreover, the genes involved in olfaction have been characterized in *Nilaparvata lugens* (Stål) (He *et al*., 2011) and *Sogatella furcifera* (Horváth) (He *et al*., 2015). *Nilaparvata lugens* showed antennal responses in electrophysiological tests for several compounds, including the green leaf complex, monoterpenes such as linalool, sesquiterpenes and salicylates (Youn, 2002). Also, the affinity of the odorant binding proteins in the antennae lumen of *N. lugens* was confirmed for several rice volatiles, including terpenes such as myrcene, α-pinene, limonene, β-caryophyllene and green leaf complex volatiles (He *et al*., 2011). *Sogatella furcifera* preferred rice plants that released highest amounts of green leaf volatiles (Wang *et al*., 2015).

In this study, we analysed the VOCs emitted constitutively by three maize germplasms that could act as odour guides determining host-selection. We studied a temperate, a tropical hybrid and a landrace that were reported to have different susceptibility to CSS and MRCV (Pionner, personal communication). We compared olfactory orientation of the corn leafhopper *D. maidis* and the corn planthopper, *P. maidis*, to the suite of three maize germplasms through free choice tests in an olfactometer. We chose to exclude the influence of vision in our trials, by covering the view of the plant, in order to analyse the role of volatile cues alone. Additionally, we tested if (±)-linalool, the compound dominating the volatile profile of the temperate germplasm, possesses a role in hoppers orientation. We predicted that (i) the three maize germplasms would have different volatile profiles, (ii) *D. maidis* and *P. maidis* would discriminate the germplasms based only on their emitted VOCs and (iii) (±)-linalool is one of the volatiles involved in host-selection by the studied hopper species.

Methods and materials

Insects and maize plants

Dalbulus maidis colony was established with individuals collected in Los Nogales, Tucumán, Argentina (26°42′S–65°13′W; 588 m a.s.l.). *Peregrinus maidis* colony was established with individuals from Cabeza de Buey, Salta, Argentina (24°48′S–65°02′W; 771 m a.s.l.). Both colonies have been maintained in the laboratory for several years and are periodically refreshed with wild insects to avoid inbreeding. Individuals used in the behavioural tests were obtained from pathogen free colonies that were reared under laboratory conditions for at least two generations.

Adult hoppers were placed in breeding cages (50 × 50 × 50 cm), made of aluminium with the lateral and upper sides covered with nylon mesh (organdy type). Potted maize plants were used as food source and for reproduction. The maize germplasm Leales 25 Plus was used for maintenance of the colonies, and they were reared in a greenhouse at San Miguel de Tucumán (26°4835.6′S–65°1424.6′W; 500 m a.s.l.) under the following conditions: temperature between 20 and 30°C, the natural photoperiod and no humidity control.

Two maize hybrids, P1780YR (temperate), P30B39HR (tropical) and the landrace sweet white maize ‘maizón’ (SWM) were selected because we were informed by the seed supplier they have different susceptibility to CSS (Pionner, personal communication). Maize plants were planted in pots (6.3 dm^3) with commercial soil and left under greenhouse conditions as described above, isolated until analysis.

Volatile collection and chemical analysis

Headspace samples were taken by enclosing intact plants with two fully unfolded leaves (V2) into a 2 litres glass recipient. Charcoal-filtered air was pushed into the recipient with an aquarium air pump and then pulled using a suction pump at a constant rate of 0.5 litres min^{-1}. Air leaving the recipient passed through a volatile collection trap (30mg HayeSep Q) where volatiles were collected. Plants were illuminated from above with blue and red LED lamps and a high-pressure metal halide lamp, light intensity 350 µmol m^{-1} s^{-1}. Seven system blanks were also performed in order to exclude contaminant products from the list of volatiles. After a sampling period of 6 h (between 10:00 and 16:00 h), the volatile collection traps were eluted with 150 µl of dichloromethane containing 5 ng of dodecane as an internal standard.

Volatile samples were analysed by coupled gas chromatography-mass spectrometry (GC/MS) (Agilent 7890 instrument coupled with an Agilent 5977 selective mass detector). A DB5MS capillary column was used (0.25-mm i.d., film thickness 0.25 µm). Samples (1 µl) were injected at 240°C in a splitless mode. Helium was used as a carrier gas at 0.75 ml min^{-1}. The column temperature was held at 35°C for 1 min, and then increased at a rate of 5°C min^{-1} until it reached 100°C, then 12°C min^{-1} until 230°C. Finally, the temperature was held at 230°C for 10 min. Compounds were identified by computer matching with commercial mass spectra libraries (NBS75K, NIST 98, WILEY275) and published data (Adams, 2007); comparison of their kovats retention index on a DB5MS column and by comparison of retention times with authentic standards: (±)-linalool, D-limonene, β-myrcene, β-*cis*-ocimene, *trans*-β-caryophyllene, β-elemene, α-humulene, nerolidol and the alkane series. Data were collected with ChemStation software (Hewlett-Packard) and the detected volatiles were quantified on the basis of their peak area in comparison with the area of the internal standard.

Olfactometer bioassays

The attractiveness of *D. maidis* females (3–6 days old) and macropterous *P. maidis* females (3–6 days old) to volatile compounds released by V2 maize plants was evaluated in olfactory dual choice tests. Behavioural recordings were carried out using static olfactometers (no air flow), with the odour sources placed in opposite directions and releasing one female at a time. The system consisted of a central releasing chamber (5.5 × 5.5 × 2 cm) and two opposite side arms (9 cm long, 1 cm diameter) connected to glass containers (20 × 5 × 5 cm) that housed a whole plant of a given maize germplasm (Supplementary material). The pots with commercial soil were left out of the glass container, and that side of the container was closed with a plastic guillotine. The side of the glass container facing the central releasing chamber was white to avoid the use of visual cues. Bioassays were performed between 9 AM and 5 PM hours under laboratory conditions (25°C, 50–70% RH illuminated from above with LED tubes). Several tests were conducted in parallel, with blank experiments running simultaneously. Olfactometers were cleaned with acetone after each experiment and the maize plants were replaced for every new replicate. *Dalbulus maidis* females were starved for 2 h before the assays. *Peregrinus maidis* females were left overnight for the same purpose. Bioassays lasted 1 h for *D. maidis* (under continuous observation), and 8 h for *P. maidis* (checking the experiment every 2 h). The time spent in the central part of the olfactometer, where insects were released, was also recorded for *D. maidis*. The first choice of each female was recorded when it moved more than 4 cm towards the odour source in the olfactometer arm and did not return to the central part, otherwise it was scored as 'no choice'. In both cases, insects could reach the plant if they passed the connecting tube, but *D. maidis* females were removed when they reached the end of the connecting tube, shortly after they made a choice, because they tended to move fast to the odour source. At least 40 replicates were performed for *D. maidis* and 30 replicates for *P. maidis*. A control experiment was also performed contrasting maize plants (SWM) vs. air, with 38 replicates for *D. maidis* and 23 replicates for *P. maidis*.

Bioassay with linalool

This compound was assayed alone since it is released in highest amounts by the temperate and SWM germplasms. (±)-Linalool was prepared from linalyl acetate according to Theodorou *et al*. (2007). Briefly, 300 mg of linalyl acetate where dissolved in 6 ml of a solution of methylene chloride (CH_2Cl_2) and methanol (MeOH) 90:10. A solution of 3 N NaOH was added and left to react under continuous stirring. After 4 h, solvents were evaporated under vacuum, and the residue was resuspended in 5 ml of H_2O and extracted four times with CH_2Cl_2. The organic extracts were reunited, filtrated and evaporated to yield 230 mg of (±)-linalool, confirmed by GC/MS analysis.

A 0.0001% solution of (±)-linalool was prepared in ethyl acetate and 100 µl were applied on filter paper disks for bioassay purposes. In a preliminary test, one of these filter paper discs was placed together with one plant of the tropical hybrid inside a 2 litre glass recipient to collect volatiles as previously described. Extracts were then analysed by GC/MS. This test confirmed that the release of linalool by filter paper was in accordance with the amounts of linalool released by the temperate maize plants (Supplementary material). Two kinds of assays were performed with this solution, linalool against solvent blanks and the tropical maize germplasm plus linalool vs tropical maize plus solvent. The two choice bioassays were conducted as previously described with both hopper species.

Statistical analyses

For VOCs analysis, peaks that appeared in the system blanks were discarded. VOC data means were compared with one-way analysis of variance (ANOVA) after normalization to log-normal distributions ($P < 0.05$). Homogeneity of variance and normality were checked using Bartlett's and Shapiro–Wilk tests, respectively. When a given compound was not detected in one of the germplasms, data were analysed by means of unpaired *t*-test between two germplasms. Mean pairwise comparisons were conducted using Tukey honestly significant difference. If ANOVA assumptions were not met, Kruskal–Wallis test was performed. All the compound classes (aromatic hydrocarbons, monoterpenes, sesquiterpenes, aliphatic aldehyde, ketone, alkanes, homoterpenes and salicylates) were used as variables to perform principal component analysis (PCA). Female choices in the olfactometer were compared by Chi-square goodness-of-fit test (χ^2) ($P < 0.05$) using XLSTAT® 19.6.

Results

Chemical characterization

The volatile fraction collected by headspace sampling of V2 maize plants allowed the identification of several substances and the characterization of the VOC pattern of each maize germplasm. All three types of maize differed qualitatively and quantitatively in their constitutive volatile compounds. We identified 42 VOCs in detectable amounts in at least four samples of a germplasm (table 1). There were differences in the total amounts of volatiles released ($F = 3.8$, df = 2_{18}, $P = 0.042$). The temperate hybrid released significantly more VOCs than the tropical hybrid ($P = 0.037$). SWM was not significantly different from both hybrids ($P > 0.050$) (fig. 1). VOCs fell into seven different categories: aromatic hydrocarbons, monoterpenes, sesquiterpenes, aliphatic, alkanes, homoterpenes and salicylates. We found 22 common volatiles. In multiple comparisons between the three germplasms, the release of two VOCs was significantly different; (±)-linalool ($F = 66.902$, df = 2_{18}, $P < 0.001$) (fig. 1) and nerolidol ($F = 4.008$, df = 2_{18}, $P = 0.036$). Linalool was released in highest amounts by the temperate hybrid and SWM (table 1). The release of the following compounds was not significantly different between SWM and the temperate hybrid (*t*-test, $P > 0.05$), but they were not detected in the tropical hybrid: β-myrcene, methyl salicylate, decanal, unknown 6, tridecane, β-elemene, caryophyllene, β-gurjunene, geranyl acetone, α-humulene, ar-curcumene, α-muurolene, 2-isopropyl-5-methyl-9-methylenebicyclo[4.4.0]dec-1-ene, (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-decatetraene (TMTT), cadalene, eicosane and unknown 7 (table 1).

PCA explained 81.9% of the total variation (fig. 2). Temperate maize was positively correlated with a greater abundance of monoterpenes, homoterpenes and methyl salicylate, whereas SWM was positively correlated with sesquiterpenes, alkanes and aromatic compounds. Tropical maize, on the other hand, was not related to monoterpenes, sesquiterpenes or homoterpenes (fig. 2). The first axis of PCA accounted for 56.2% of the total variation (eigenvalue 3.37) and was positively correlated with all the compound classes. The second component explained 25.7% of the variation (eigenvalue 1.54) and was related to monoterpenes, homoterpenes and salicylates, and negatively related to alkanes, sesquiterpenes and aromatic compounds.

Olfactometer bioassays

A majority of the females from both species, *D. maidis* and *P. maidis*, made a choice for the olfactometer arm with the odour source consisting on a maize plant. When offered a maize plant vs. clean air, *D. maidis* females spent an average of 20.5 min (±14.8) on the central part of the olfactometer, where insects were released, and more than 70% preferred the side with the maize plant ($\chi^2 = 6.125$, df = 1, $P = 0.013$). If no such odour is offered, most *D. maidis* females remained in the central releasing chamber during the 60-min test period. *Peregrinus maidis* females also preferred the side with the plant ($\chi^2 = 4.545$, df = 1, $P = 0.033$), but they spent a much longer time in the centre of the olfactometer until they made a choice for an olfactometer arm; 50% remained in

Table 1. Volatiles emitted constitutively by the three maize germplasms ($N = 7$).

No.	Compound	RI	Type	SWM	Temperate	Tropical	Identification
1	Unknown 1	798	Aliphatic	–	0.26 (±0.16)a	0.41 (±0.12)a	
2	Ethylbenzene	862	Aromatic	0.31 (±0.15)a	0.32 (±0.17)a	0.38 (±0.09)a	MS, RI
3	Propylbenzene	954	Aromatic	0.24 (±0.09)a	0.12 (±0.08)a	0.09 (±0.05)a	MS, RI
4	*m*-Ethyltoluene	964	Aromatic	1.24 (±0.38)a	0.43 (±0.39)a	0.34 (±0.21)a	MS, RI
5	Benzene, 1,3,5-trimethyl-	969	Aromatic	0.39 (±0.18)a	1.19 (±0.11)a	0.12 (±0.05)a	MS, RI
6	β-Myrcene	989	Monoterpene	0.09 (±0.09)a	0.54 (±0.26)a	–	MS, RI, S
7	Benzene, 12,4-trimethyl-	993	Aromatic	1.60 (±0.53)a	0.54 (±0.45)a	0.50 (±0.19)a	MS, RI
8	2,6-Dimethyl-nonane	1024	Aliphatic	0.44 (±0.16)a	0.53 (±0.14)a	0.36 (±0.14)a	MS, RI
9	Limonene	1026	Monoterpene	0.42 (±0.22)a	0.76 (±0.37)a	0.65 (±0.14)a	MS, RI, S
10	β-*cis*-Ocimene	1050	Monoterpene	0.09 (±0.05)a	0.15 (±0.08)a	0.02 (±0.02)a	MS, RI, S
11	3-Methyl-decane	1070	Aliphatic	0.03 (±0.02)a	1.18 (±0.09)a	0.22 (±0.09)a	MS, RI
12	Unknown 3	1074		0.05 (±0.05)a	0.56 (±0.24)a	0.88 (±0.35)a	
13	Benzene, 2-ethyl-1,4-dimethyl-	1085	Aromatic	0.14 (±0.06)a	–	0.04 (±0.04)a	MS, RI
14	Linalool	1100	Monoterpene	2.42 (±0.47)a	7.03 (±0.68)b	0.27 (±0.21)c	MS, RI, S
15	DMNT	1116	Homoterpene	0.09 (±0.09)a	0.67 (±0.32)a	0.23 (±0.14)a	MS, RI
16	Unknown 4	1124		–	0.33 (±0.14)a	0.27 (±0.11)a	
17	Unknown 5	1173		–	0.43 (±0.13)a	0.77 (±0.31)a	
18	Methyl salicylate	1195	Salicylate	0.26 (±0.09)a	0.16 (±0.04)a	–	MS, RI
19	Decanal	1205	Aliphatic aldehyde	1.23 (±0.42)a	0.36 (±0.24)a	–	MS, RI
20	Unknown 6	1282		0.12 (±0.05)a	0.07 (±0.04)a	–	
21	Tridecane		Alkane	0.24 (±0.16)a	0.04 (±0.03)a	–	MS, RI, S
22	(+)-Cycloisosativene	1374	Sesquiterpene	0.35 (±0.15)a	0.31 (±0.03)a	0.31 (±0.08)a	MS, RI
23	Ylangene	1377	Sesquiterpene	0.29 (±0.13)a	0.23 (±0.06)a	0.17 (±0.10)a	MS, RI
24	α-Copaene	1382	Sesquiterpene	0.55 (±0.17)a	0.38 (±0.21)a	0.28 (±0.11)a	MS, RI
25	β-Elemene	1395	Sesquiterpene	0.08 (±0.03)a	0.02 (±0.02)a	–	MS, RI, S
26	Tetradecane		Alkane	0.20 (±0.06)a	0.23 (±0.13)a	0.09 (±0.05)a	MS, RI, S
27	*trans*-β-Caryophyllene	1427	Sesquiterpene	0.09 (±0.04)a	0.10 (±0.10)a	–	MS, RI, S
28	β-Gurjunene	1441	Sesquiterpene	0.37 (±0.14)a	0.30 (±0.18)a	–	MS, RI
29	Geranyl acetone	1458	Ketone	0.19 (±0.08)a	0.06 (±0.06)a	–	MS, RI
30	α-Humulene	1459	Sesquiterpene	0.15 (±0.05)a	0.05 (±0.05)a	–	MS, RI, S
31	ar-Curcumene	1490	Sesquiterpene	0.22 (±0.11)a	0.03 (±0.03)a	–	MS, RI
32	Pentadecane		Alkane	0.16 (±0.08)a	0.13 (±0.08)a	0.03 (±0.03)a	MS, RI
33	α-Muurolene	1506	Sesquiterpene	0.15 (±0.07)a	0.08 (±0.05)a	–	MS, RI
34	δ-Amorphene[a,b]	1513	Sesquiterpene	0.15 (±0.09)	–	–	MS, RI
35	2-Isopropyl-5-methyl-9-methylene-bicyclo-1-decene[4.4.0]	1523	Sesquiterpene	0.13 (±0.04)a	0.08 (±0.03)a	–	MS, RI
36	Calamenene[b]	1531	Sesquiterpene	0.53 (±0.16)a	0.35 (±0.13)a	0.25 (±0.07)a	MS, RI
37	Nerolidol	1543	Sesquiterpene	0.12 (±0.04)a	0.02 (±0.02)a	0.02 (±0.02)a	MS, RI, S
38	TMTT[b]	1580	Homoterpene	0.11 (±0.04)a	0.12 (±0.08)a	–	MS, RI
39	Cadalene	1689	Sesquiterpene	0.12 (±0.05)a	0.10 (±0.05)a	–	MS, RI
40	Octadecane		Alkane	0.08 (±0.03)a	0.11 (±0.11)a	0.08 (±0.04)a	MS, RI, S
41	Unknown 7	1849	Homoterpene	0.25 (±0.07)a	0.23 (±0.15)a	0.03 (±0.03)ab	
42	Eicosane		Alkane	0.10 (±0.03)a	0.06 (±0.04)a	–	MS, RI, S
	Total VOCs			14.10(±3.06)ab	17.54 (±3.28)a	7.16 (±1.33)b	

DMNT, (3*E*)-4,8-dimethyl-13,7-nonatriene; TMTT, (3*E*,7*E*)-4,8,12-trimethyl-1,3,7,11-decatetraene.

Differences between germplasms were determined using one-way ANOVA after normalization to log-normal distributions. Mean pairwise comparisons were conducted using Tukey honestly significant difference. Means followed by the same letter within a line are not significantly different ($P < 0.05$) (±SE). Data expressed as ng h^{-1}. RI = Kovats retention index determined according to *n*-alkanes on a DB-5MS capillary column. Identification based on mass spectra (MS), retention index and authentic standards (S).

[a] Coelution of another sesquiterpene alcohol (MW 220, $C_{15}H_{24}O$).

[b] Tentative identification.

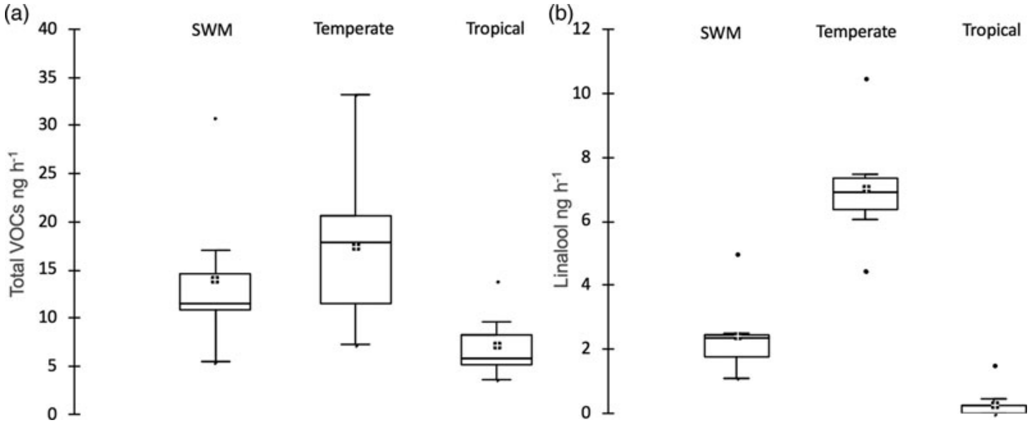

Fig. 1. (a) Total VOCs emitted constitutively by SWM and the temperate and tropical maize hybrids. (b) Amount of linalool emitted by the three germplasms. Bars represent SD.

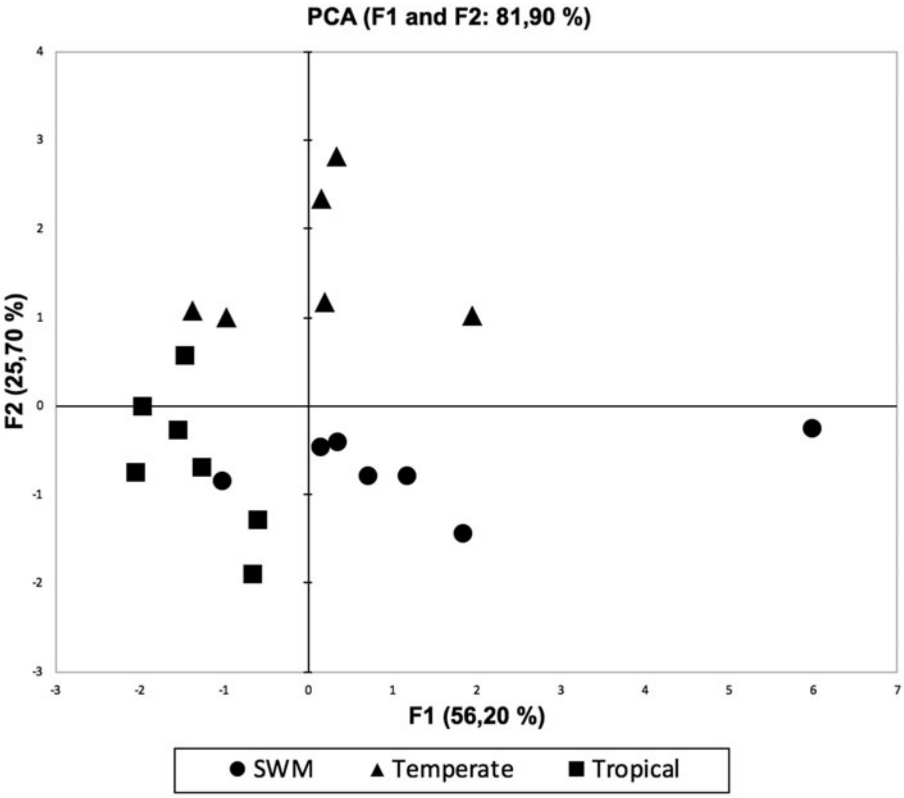

Fig. 2. PCA representing the association among the 21 cases belonging to three maize germplasms on relative amounts of odours emitted. The first two axes account for 56.2 and 25.7% of the total variation.

the central part after 4 h, and by 8 h, 72.7% have moved to the odour plant source, while 27.3% had moved to the side with no plant.

When offered two different germplasms in each side of the olfactometer, *D. maidis* preferred seedlings with temperate genetic background (73.7%) instead of tropical background ($\chi^2 = 8.526$, df = 1, $P = 0.003$), and did not discriminate between SWM and tropical maize ($\chi^2 = 0.105$, df = 1, $P = 0.746$) or SWM and the temperate hybrid ($\chi^2 = 0.947$, df = 1, $P = 0.330$) (fig. 3).

On the other hand, *P. maidis* chose seedlings with tropical genetic background (70.7%) over temperate maize ($\chi^2 = 7.048$, df = 1, $P = 0.008$); significantly chose SWM (72.7%) over temperate ($\chi^2 = 6.818$, df = 1, $P = 0.009$) and there was a slight preference for SWM (62.9%) over tropical maize although not significant ($\chi^2 = 2.314$, df = 1, $P = 0.128$) (fig. 3).

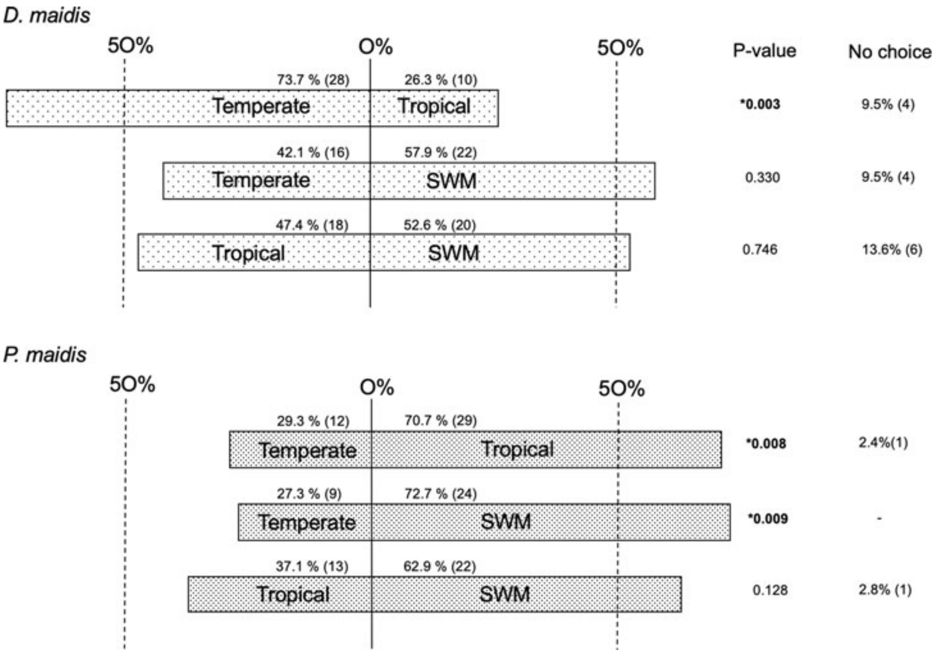

Fig. 3. First choice (%) between different germplasms in olfactometer. Chi-square goodness-of-fit test (χ^2) $*P < 0.05$.

Bioassays with linalool

(±)-Linalool was assayed alone since it is released in differential amounts for all three genotypes (higher for temperate, lower for SMW and almost null for tropical) (table 1, fig. 1). A pure 0.0001% linalool solution failed to produce a behavioural effect both on *D. maidis* ($\chi^2 = 0.133$, df = 1, $P = 0.715$), and on *P. maidis* ($\chi^2 = 0.676$, df = 1, $P = 0.411$) (fig. 4). But, when both species were offered the 0.0001% linalool solution plus the tropical hybrid, providing other maize contextual cues, *D. maidis* chose the tropical hybrid plus linalool ($\chi^2 = 4.000$, df = 1, $P = 0.045$), whereas *P. maidis* had a slight preference, although not significant, for the tropical hybrid plus solvent ($\chi^2 = 2.000$, df = 1, $P = 0.157$) (fig. 4).

Discussion

Analysis of the VOCs collected from the three maize germplasms showed quantitative and qualitative variations in the composition of the blend. Both hopper species, *D. maidis* and *P. maidis* were able to discriminate between the two maize hybrids by the use of volatile cues in the absence of supplementary visual cues.

The temperate and the tropical hybrid differed significantly in the total amount of volatiles released. SWM was not significantly different in terms of VOCs production from both hybrids. All the identified VOCs were previously cited for maize (Krokos *et al.*, 2002; Oluwafemi *et al.*, 2012; Robert *et al.*, 2013; Molnár *et al.*, 2015; Potter *et al.*, 2015). The temperate hybrid was very different from the tropical hybrid in qualitative volatile composition, particularly because the tropical hybrid lacked many compounds that were present in the temperate one.

As expected, tropical maize plants presented low variability between individuals in terms of VOCs quantities and the identity of the compounds released. SWM, on the other hand, had more variability between individuals, since landraces are crop cultivars that are usually genetically diverse and have been selected by local environments and farmers over many generations (Davila-Flores *et al.*, 2013). Surprisingly, the temperate hybrid presented considerable variability between individuals. Hybrids are the result of selective breeding programmes and are usually unable to produce viable seeds after a couple of generations. It is possible that this hybrid has retained a high degree of genetic variability during its breeding programme.

The corn leafhopper, *D. maidis*, has a long history of coevolution with maize ancestors, the teosintes and maize landraces in tropical environments (Nault, 1983). Tropical hybrids are developed from these landraces that have been subjected to high CSS and herbivore pressures and they are supposed to be more resistant to CSS, which was associated, at least partially, to lower incidence of disease vectors (Carpane & Ingrassia, 2012). On the other hand, for the more polyphagous corn planthopper, *P. maidis*, sorghum would be the ancestral host and *P. maidis* would have adapted only in post-Columbian times to maize as a host (Nault, 1983).

Based on the origin of the germplasm and also on information from the seed supplier, we expected the tropical hybrid to be the less preferred by the corn leafhopper. Accordingly, *D. maidis* chose the temperate hybrid over the tropical hybrid but failed to discriminate between the temperate hybrid and SWM and the tropical hybrid and SWM. The most abundant monoterpene released by the temperate hybrid is (±)-linalool. Other monoterpenes such as α-pinene and camphene are known to be active towards the leafhopper *Amrasca devastans* (Distant) (Saxena & Saxena, 1974). *Dalbulus maidis* was not attracted by a pure 0.0001% linalool solution, in the order of magnitude released by the temperate hybrid. This result suggested that other contextual cues could be necessary to obtain a response, so the tropical hybrid plus linalool and the tropical hybrid plus solvent were contrasted, and this time the tropical

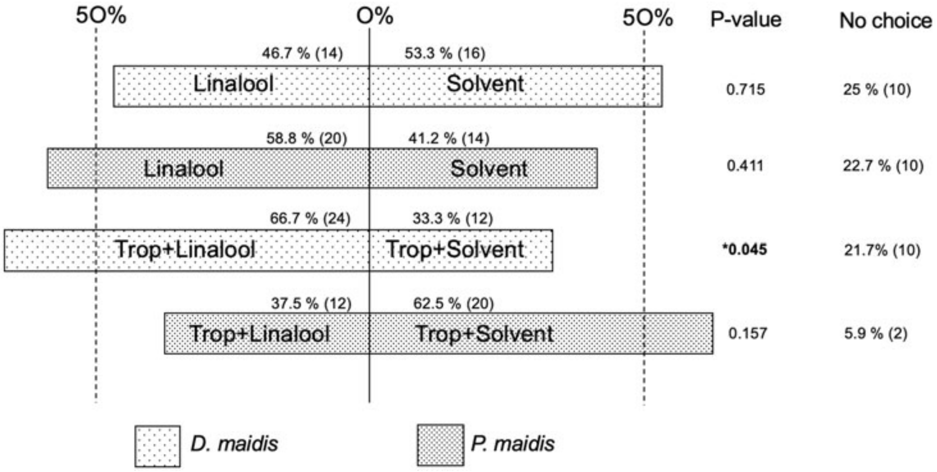

Fig. 4. First choice (%) in olfactometer between 0.0001% linalool vs. solvent and tropical hybrid plus 0.0001% linalool vs. tropical hybrid plus solvent. Chi-square goodness-of-fit test (χ^2) $*P < 0.05$.

hybrid plus 0.0001% linalool was significantly preferred. The temperate hybrid could be more attractant to the leafhopper than the tropical hybrid because of a blend of compounds, that includes linalool. In that case, the tropical hybrid would be less preferred because of decreased attraction, that could be an adaptation in an environment with high *D. maidis* pressures.

Peregrinus maidis females, chose the tropical hybrid and SWM over the temperate hybrid. As mentioned before, this last hybrid releases higher amounts of monoterpenes (β-myrcene, β-*cis*-ocimene and linalool) and also homoterpenes. Many terpenoids are bitter defence compounds. Particularly, (*E*)-caryophyllene, TMTT and methyl salicylate, all present in the temperate hybrid but not in the tropical hybrid, were previously identified as volatile semiochemicals involved in plant defence against other sucking insect pests, including the leafhopper *C. storeyi* (Oluwafemi *et al.*, 2011). The more generalist *P. maidis* would choose the less defended tropical hybrid. SWM might also attract *P. maidis* being chemically similar to the tropical hybrid. When the 0.0001% linalool solution in combination with the tropical hybrid was offered to *P. maidis*, the side with no added linalool was slightly preferred, but other compounds could also be responsible for making the temperate hybrid less attractive to the planthopper.

Most *P. maidis* females responded after at least 4 h in the olfactometer, even after being starved for at least 14 h. This behaviour could be related to the ecological role of macropterous females that can spend several hours without feeding, in search for a suitable host. *D. maidis* females made their choices faster, usually about 20 min after being released. The lack of a visual stimulus could be responsible for the long time both insects spent in the olfactometer.

Although most of the literature suggest that the role of olfactory cues in long-range orientation within Auchenorrhyncha is likely to be supplementary to visual cues (Todd *et al.*, 1990; Fereres & Moreno, 2009; La Grange *et al.*, 2017; Zhang *et al.*, 2017), our results suggest that olfaction might play a role in host selection within short distances, where responsiveness to other host plant cues might arise. Therefore, both *D. maidis* and *P. maidis* could also select their host plants based on the emitted VOCs. Ultimately, there is potential to develop a behavioural manipulation method in agronomic practices, such as trap plants or a push–pull strategy, where volatile cues are used to push insects away from important crop plants and attract them to a trap or trap crop (Cook *et al.*, 2007; Hassanali *et al.*, 2008), combining visual and olfactory cues.

Supplementary material

The supplementary material for this article can be found at https://doi.org/10.1017/S000748531900004X.

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