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Banana Tree Infected with *Banana Bunchy Top Virus* Attracts *Pentalonia nigronervosa* Aphids Through Increased Volatile Organic Compounds Emission

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Abstract

Banana plants are affected by various viral diseases, among which the most devastating is the "bunchy top", caused by the *Banana bunchy top virus* (BBTV) and transmitted by the aphid *Pentalonia nigronervosa* Coquerel. The effect of BBTV on attraction mechanisms of dessert and plantain banana plants on the vector remains far from elucidated. For that, attractiveness tests were carried out using a two columns olfactometer for apterous aphids, and a flight cage experiment for alate aphids. Volatile Organic Compounds (VOCs) emitted by either healthy or BBTV-infected banana plants were identified using a dynamic extraction system and gas-chromatography mass-spectrometry (GC–MS) analysis. Behavioral results revealed a stronger attraction of aphids towards infected banana plants (independently from the variety), and towards the plantain variety (independently from the infection status). GC–MS results revealed that infected banana plants produced VOCs of the same mixture as healthy banana plants but in much higher quantities. In addition, VOCs produced by dessert and plantain banana plants were different in nature, and plantains produced higher quantities than dessert banana trees. This work opens interesting opportunities for biological control of *P. nigronervosa*, for example by luring away the aphid from banana plants through manipulation of olfactory cues.

Keywords *Musa* spp. · Phytovirus · Behavior · Volatile organic compounds · Metabolites · Biological control

Introduction

Banana viral diseases are responsible for major economic damages to producers (Kumar et al. 2015). They constitute a major constraint in banana fruit production and threaten worldwide germplasm distribution (Mobambo et al. 2010; Mukwa et al. 2014; Shiragi et al. 2010; Thomas et al. 1994; Walangululu et al. 2010). Banana bunchy top disease, caused by the *Banana Bunchy Top Virus* (BBTV), is recognized as the most devastating viral disease of banana plants in the world (Chandrassekar et al. 2011; Qazi 2016; Thomas and Iskra-Caruana 2000), sometimes resulting in 100% yield loss (Qazi 2016). BBTV is transmitted by the banana aphid, *Pentalonia nigronervosa* Coquerel (Hemiptera: *Aphididae*). BBTV belongs to the *Nanoviridae* family, genus *Babuvirus*, whose genome is composed of several segments of single-stranded circular DNA, encapsidated in small isometric particles (18–20 nm), which makes it one of the smallest phytoviruses (Burns and Dale 1995; Mukwa et al. 2016; Stainton et al. 2015; Timchenko and Bernardi 2007). Currently, BBTV is present in Africa, Asia, and Australia, while its vector is located in all regions of the world, even where BBTV is not yet reported, such as in South America and Europe (CABI 2021).

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Infected plants show dwarfism, narrow leaves, chlorosis of leaf margins, and discontinuous dark-green streaks on leaves, petioles, and pseudotem. The leaves of infected plants become progressively smaller and stand more erect, giving the plant a bunchy appearance (Gatsinzi 1987). In the plant, BBTV is restricted to phloem tissues. In infected plants, the cells surrounding the phloem vessels contain an abnormal number of chloroplasts, giving rise to the macroscopic symptoms of dark green streaks. After infection, BBTV replicates and gradually accumulates in all parts of the plant, except in leaves formed before infection, in which the virus is present, but does not replicate. This explains the fact that the vector is not able to acquire the virus from these leaves (Hafner et al. 1995; Iskra-Caruana 2003).

The vector aphid *P. nigronervosa* transmits the virus in a persistent, circulative and non-propagative manner (Iskra-Caruana 2003; Anhalt and Almeida 2008). This implies a lifelong retention of the virus in the vector, with a relatively long acquisition time during a meal on an infected plant (a few hours to many days; persistent transmission). After its ingestion by the vector, the virus reaches the intestine, crosses the intestinal wall, and diffuses from the hemolymph into the salivary glands. There it becomes transmissible to a new plant (circulative transmission), without any additional viral replication during transfer (non-propagative transmission) (Gray et al. 2014; Raccah and Fereres 2009).

The search and selection of the host plant by aphids remain essentially facilitated by volatile organic compounds (VOCs) emitted by plants (Bernasconi et al. 1998; Pickett et al. 2013; Piesik et al. 2013), even if in some situations, visual stimuli (color, movement, shape) seem to be involved (Döring 2014; Leather 2014). Plant VOCs are detected by insect olfactory systems located on their antennae (Bernasconi et al. 1998; Piesik et al. 2013; Hardie et al. 1995). In herbivorous insects such as aphids, VOCs influence host plant searching behavior, which can lead to potential virus transmission (Berenbaum 1995; Herrbach 1985; Whittaker and Feeny 1971). Consequently, variation in the composition (quality and quantity) of VOCs emitted by their host plants can trigger changes in aphid feeding preferences (Peccoud et al. 2010; van Emden 1973).

Previous studies showed that VOC emissions vary depending on the plant's viral infection status (Bosque-Pérez and Eigenbrode 2011; Chaudhry et al. 1998). For example, Eigenbrode et al. (2002) showed that the profile of VOCs emitted by potato plants (*Solanum tuberosum*) infected with *Potato Leafroll Virus* (PLRV) differs to that of healthy plants in terms of composition and concentration. The study by Jiménez-Martínez et al. (2004) shows that wheat plants infected with Barley Yellow Dwarf Virus (BYDV) emit VOCs in greater concentrations than healthy wheat plants. Virus-induced differences in VOC emissions may modify aphid preference to some kind of host plants. The aphid *Myzus persicae*, is preferentially attracted to potato plants (*S. tuberosum*) infected by PLRV compared to healthy plants or plants infected by other viruses (Bosque-Perez and Eigenbrode 2011; Eigenbrode et al. 2002). The same situation occurs with *Rhopalosiphum padi*, an aphid that transmits BYDV in wheat (Jimenez-Martinez et al. 2004; Srinivasan et al. 2006). On the other hand, some aphids avoid infected plants, when they are hosts of lower quality. This is the case for example in *Cucurbita pepo*, where plants infected with the *Cucumber Mosaic Virus* (CMV) are of low quality for aphid vectors, especially *My. persicae* and *Aphis gossypii*, compared to healthy plants (Mauck et al. 2010). It is suggested that CMV manipulates the plant to induce the production of volatile compounds that falsely attract vectors to infected plants that they then leave quickly (Mauck et al. 2010). In addition, the preference of vectors for infected plants may turn into a preference for uninfected plants after the acquisition of the pathogen, thereby accelerating the spread of the disease (Carmo-Sousa et al. 2014, 2016; Eigenbrode et al. 2018; Ingwell et al. 2012; Rajabaskar et al. 2014).

The topic of chemical interactions between insects and their biotic environment is currently the subject of increasing research for biocontrol of phytophagous insects (Bosque-Pérez and Eigenbrode 2011; Chesnais et al. 2019a, b; Mauck et al. 2010; Xu et al. 2018). The conclusions of Eigenbrode et al. (2002, 2018) and Mauck and Chesnais (2020) tend to reinforce the "vector manipulation hypothesis", predicting that a virus will promote its propagation from plant to plant by influencing the selection behavior and movement of the vector (Ingwell et al. 2012; Roosien et al. 2013). Exploring ways of manipulating the behavior of BBTV vectors is especially relevant in the current context of increasing resistance to synthetic insecticides and issues regarding their negative impact on the environment and human health (Edwards and Tchounwou 2005; Penrose et al. 1994). Recently, Berhal et al. (2017) characterized the VOCs released by the aerial part of healthy banana seedlings. However, the impact of BBTV on the attractiveness of banana plants (*Musa* spp.) to *P. nigronervosa* remains unknown.

Our study aimed at better understanding the interaction between banana plants of dessert and plantain varieties, infected or not by the BBTV, and the aphid vector. In particular, we addressed the question of whether BBTV is capable of modifying the VOC emissions of banana trees to influence *P. nigronervosa* attraction. We hypothesize that the composition and quantities of VOCs emitted by banana trees are affected by BBTV infection and that infected banana trees emit VOCs are more attractive to *P. nigronervosa* than those emitted by healthy plants. Healthy and infected young plants of two most representative varieties of bananas were used in this work; Cavendish dessert bananas (AAA genome) and Plantain Pacific bananas (AAB genome) (Lorenzen et al. 2010; Ploetz 2015; Simmonds 1962), to

assess the influence of the virus on VOC emissions and the behavior of *P. nigronervosa*. From a more applied point of view, an additional goal to this study is to determine if some VOCs profile could be used to repel or falsely attract banana aphids.

Material and Methods

Insects and Plants

Pentalonia nigronervosa colony was obtained from a parthenogenetic female collected from a healthy banana tree in the province of South Kivu (Democratic Republic of the Congo), and continuously reared on live bananas, disease-free, and planted in pots (Thermoformed red MCI 17:2L pot) on a potting soil substrate. Aphids on banana plants were kept in cages (200 × 100 × 100 cm) of small mesh nets, placed in air-conditioned chambers at 25 ± 2 °C, a relative humidity of 30 ± 5%, and an artificial 12 h/12 h photoperiod. Experiments were also carried out under these conditions. Before their use in each attractiveness test, adult aphids were taken from banana plants and placed in glass Petri dishes for at least 8 h to starve them. Alate aphids were obtained when the density of the aphid population increased sharply, or when the quality of bananas decreased significantly (Braendle et al. 2006; Williams and Dixon 2007).

The plant material was constituted of dessert bananas of cultivar Cavendish (strict triploid *M. acuminata*—AAA), and plantains of the Pacific cultivar (hybrids and triploids *M. balbisiana*—AAB), either symptomatic (with symptoms of BBTV) or asymptomatic (without disease symptoms). This resulted in four plant treatments that were used for both the behavioral experiment with aphids and for VOC extraction and identification: Healthy Dessert Bananas (HDB), Healthy Plantain Bananas (HPB), Infected Dessert Bananas (IDB), Infected Plantain Bananas (IPB). Plants were identified and collected in peasant plantations in South Kivu in the Democratic Republic of the Congo (Dowiya et al. 2009), with the support of the International Institute of Tropical Agriculture-IITA/Kalambo (Bukavu, RD Congo). All these plants were maintained and multiplicated in the tropical greenhouse (greenhouse no. 13; G2) of the Université catholique de Louvain (Louvain-la-Neuve, Belgium) by the PIF technique (*Plantes Issues de Fragments de tiges*) (Kwa 2003, 2009; Meutchieye 2009; Mbunzu et al. 2019; Sadom et al. 2010). They were irrigated daily, until they were 40–60 days of age (4–6 leaf stage), before they were used in bioassays with apterous and alate aphids, and assessment of VOCs. Transmission of the virus by mechanical inoculation has never been successful (Lepoivre 2003; Thomas et al. 1994), however, BBTV accumulates in the pseudostem, in the basal meristem of the bulb, and in the leaf (Hafner et al. 1995). Therefore, suckers from an infected strain are automatically infected and show severe BBTV infection symptoms (van Regenmortel et al. 2000; Thomas and Iskra-Caruana 1999). The infected plants were obtained directly from the bulbs of infected banana plants. Each plant was tested twice by PCR (Supplementary Table S1) to confirm the genotype (Supplementary Figure S1) and the infection status (Supplementary Figure S2).

Attraction of *P. nigronervosa*

Apterous aphids

The apterous *P. nigronervosa* attractiveness on different types of banana trees was determined using a two-column glass olfactometer (Y olfactometer), associated with an air flow, set at a pressure of 2.5–3 bars, and placed on a light table.

Banana seedlings used were in the 4th to 6th leaves stage and contained in glass bells designed for this purpose. Four choice tests were carried out: HDB–HPB, HDB–IDB, HPB–IPB, and IDB–IPB (i.e., one for each plant genotype and infection status comparison). In addition, three control choice tests were done: HDB–S (Soil) (pot containing the soil alone), HPB–S, and S–E (Empty). Each test was repeated 30 times, and within each repetition, 20 apterous adult aphids, at reproduction age, were placed at the central neutral chamber of the olfactometer. The banana plants and apterous aphids used in each repetition and each treatment had never been used before. We considered that an individual aphid had made a choice between one of two sources of VOCs when they passed the middle of the tube connecting the neutral chamber to one of two olfactory sources after 30 min of observation. To prevent odor residue remaining from one experiment (or repetition) to the next, the pots containing the plants were inverted and the olfactometer was washed and sterilized with 70% ethanol, then dried for five minutes before further reuse.

Alate aphids

The attractiveness of the different types of banana plants on alate *P. nigronervosa* was determined using a wooden cage (200 × 100 × 100 cm), equipped with an electric fan and a fluorescent lamp (photoperiod: 12 h/12 h), allowing short distance aphid flights. The front of the cage was covered with a fine mesh fabric to facilitate experimental handling.

Each test was repeated 20 times, and within each repetition, two types of banana plants at the 4th to 6th leaves stage were placed in the cage. Twenty alates aphids per cage were put in an open Petri dish, on the other side of the cage and at an equal distance from both plants (≈ 15 cm), to test their choice between the two olfactory sources.

Four tests were performed: HDB–HPB, HDB–IDB, HPB–IPB, and IDB–IPB. As for apterous aphids, two other comparisons serving as controls were done: HDB–S (pot containing the soil alone), and HPB–S.

Aphid choices were assessed by counting the number of aphids found on each of two types of banana plants 24 h after they were deposited in the cage, and each choice experiment was repeated 20 times. The banana plants and alate aphids used in each repetition and each treatment had never been used before.

VOC extraction and analysis

VOC extraction

The VOCs were collected using a dynamic headspace collection system made up of a glass enclosure (40L), hermetically sealed, and connected to a vacuum pump (Rocker 300, Vacuum Pressure Pump, 80 mBar, -HG 680 mm, 20 L. min^{-1}, NSE, GA, USA). In the glass enclosure, a live banana plant (never used before) ≈ 50 cm high (4–6 leaves) from each genotype (plantain and dessert) and each BBTV status (infected and healthy) was placed. The pots in which the banana plants were planted were covered with aluminum foil to prevent the emission of VOCs from the underground part of the plant and the VOCs of the potting soil. Another pot containing only potting soil and also covered with aluminium foil served as a control in this part of the study. All the treatments (HDB, IDB, HPB, IPB) and controls (potting soil alone) were repeated five times. Each banana plant was used only once, in a single repetition and treatment group. Each enclosure was covered with a Pyrex bell carrying two openings to which were connected two Teflon pipes (ELNEO: TFL 8 × 6 NATUR). One of the two pipes was connected to an activated carbon filter cartridge which purifies the air entering the system, and the other was connected to a bottle containing silica gel dehydrating the air rich in VOCs from the enclosure, before passing through the trap cartridge (TENAX TA wax trap, Gerstel, Mülheim an der Ruhr, Germany), capturing the extracted VOCs. The cartridge outlet was connected to the pump via an adjustable flow valve maintaining the airflow at 500 $mL.min^{-1}$. The entire extraction device was placed in an air-conditioned room, at a temperature of 25 ± 2 °C, a relative humidity of 40 ± 5%, and an artificial photoperiod of 12 h/12 h, and the VOC collection lasted 24 h.

VOC analysis

After each extraction from the four types of banana trees (HDB, IDB, HPB, IPB) and of the control, the TENAX cartridge loaded with VOCs was thermally desorbed (Thermal desorption unit, Gerstel, Mülheim an der Ruhr, Deutschland) at 280 °C for 10 min. The analysis of captured VOCs was made using Gas Chromatography (7890A, Agilent Technologies, Santa Clara, CA, USA) coupled with Mass Spectrometry (5973, Agilent Technologies, Santa Clara, CA, USA) (GC–MS). The identification of VOCs was carried out by comparing the retention time and the mass spectra of the data obtained with available standards. Quantification was performed by comparing the peak areas of the compounds with the standard peak areas (peak surfaces) provided by the Chemstation software (Agilent Technologies, Palo Alto, CA, USA). The retention times (in minutes) and peak areas (expressed in number of hits on the detector) of the chromatograms obtained served so respectively as qualitative and quantitative parameters in this comparison. The validation of the VOCs extracted for each treatment was motivated by their presence in at least four replicates out of five (De Backer et al. 2015), and by their absence in the control sample (potting soil alone). This protocol allowed comparing both the nature and the concentration of VOCs emitted by the aerial part of banana plantlets of each of the four treatments.

Statistical analyses

Comparisons of decisions made by both alate and apterous aphids between each pair of olfactory sources were carried out using Student's t-tests (the normal distribution of our data was visually assessed and confirmed using the Shapiro–Wilk test).

Biplot PCAs of the 16 detected VOCs were constructed using the *factoextra* package (Kassambara and Mundt 2017). Two PCAs representations were done; one by banana plant varieties (dessert or plantain) and one by grouping banana plants according to their infection status (infected or healthy). Ellipses were added around the barycenter of the groups using a 95% CI. After that, the Adonis function from the package *vegan* (permutational MANOVA) has been used by calculating a Jaccard distance matrix and running 999 permutations, to assess if the composition of the set of volatile compounds differed between varieties and between infection status (i.e., differences among created groups on the PCA).

Then, the effect of the variety factor (two levels) and the infection state factor (two levels), as well as that of the interaction of both factors on the quantity of each VOC emitted were analyzed. To do so, Generalized Linear Models (GLMs) were fitted to the data, for each VOC, using a negative binomial distribution family for count data. Models were tested using the Anova function of the *car* package, and a Wald statistic. Then, in a more detailed approach, we compared the mean recorded value of each volatile among the four treatments. For each of the VOCs detected and

measured, pairwise comparisons of the peak areas were performed using negative binomial GLMs, between HDB-HPB, HDB-IDB, IDB-IPB, and HPB-IPB. All analyses were carried out in R (v. 4.0).

Results

Attraction of aphids by banana plants

In the validation tests comparing the attraction of banana aphids towards a banana plant or a control (potting soil only), the apterous and alate aphids were each time more attracted by the banana plant, regardless of the genotype (Supplementary Table S2). Apterous aphids were attracted in similar ways to potting soil alone (S) or empty (E) pots (Supplementary Table S2).

The apterous adults of *P. nigronervosa* were more attracted to IDB than to HDB ($t=-5.0$, $p<0.001$, Fig. 1a), and more to IPB than to HPB ($t=-2.3$, $p=0.02$, Fig. 1b). They were also more attracted to IPB than to IDB ($t=-2.8$, $p<0.01$, Fig. 1c), and to HPB than to HDB ($t=-2.3$, $p=0.02$, Fig. 1d).

The alate adults of *P. nigronervosa* were more attracted to IDB than to HDB ($t=-5.04$, $p<0.001$, Fig. 2a), and to IPB than to HPB ($t=-6.68$, $p<0.001$, Fig. 2b). In addition, alate aphids were significantly more attracted to IPB than to IDB ($t=-2.65$, $p=0.01$, Fig. 2c), while they were not differentially attracted to HDB and HPB ($t=-1.48$, $p=0.15$, Fig. 2d). The attraction of both morphs of *P. nigronervosa* to banana plants, therefore, varies according to both the infection status and genotype of banana plants.

Identification of VOCs emitted by healthy and infected banana plants

A total of 16 volatile organic compounds were detected (Fig. 3), of which 12 VOCs were emitted by dessert bananas and 13 by plantains (regardless of the infection status). Three compounds (α-pinene, β-pinene, and limonene) were specific to dessert banana, while four compounds (4,8-dimethyl-1,3,7-nonatriene, (*E*)-β-farnesene, (*Z, E*)-α-farnesene, and alloocimene) were specifically released by plantain banana plants (infected and healthy). Nine were common between the two genotypes ((*E*)-hex-2-enal, (*E*)-β-ocimene, (*Z*)-β-ocimene, 6-methyl-3,5-heptadien-2-one, 6-methyl-5-hepten-2-one, linalool, methyl salicylate, myrcene, and nonanal), corresponding to 75% of the total for dessert bananas, 69% for plantain, and to 56% of the total of all emitted VOCs. Other compounds were identified but not retained in the final list because of their presence in the control treatment (potting soil only), and in less than four replicates out of the five (De Backer et al. 2015).

Results revealed that these VOCs varied in quality and quantity between genotypes (dessert and plantain bananas) regardless of the infection status, while they varied mainly in quantity between infected status, regardless of the genotype (Fig. 3, Table 1). Overall, the variety ($F=21.0$, $R^2=0.43$, $p<0.001$) and the infection status ($F=8.2$, $R^2=0.17$, $p<0.01$) had an effect on VOCs emitted by banana plants, with a slight interaction effect between both variables

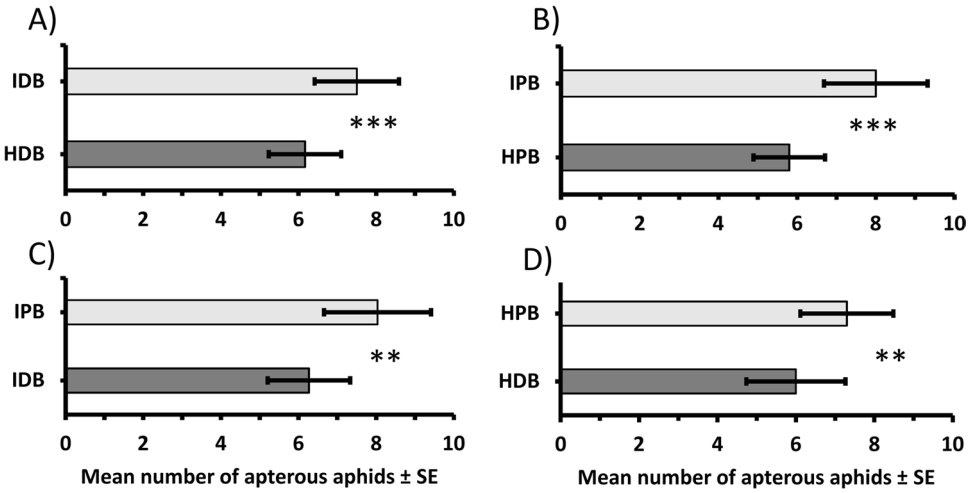

Fig. 1 Effect of banana plant treatment on the choice of apterous aphids *P. nigronervosa*: **a** Healthy Dessert Banana and Infected Dessert Banana; **b** Healthy Plantain Banana and Infected Plantain Banana; **c** Infected Dessert Banana and Infected Plantain Banana; **d** Healthy Dessert Banana and Healthy Plantain Banana. The mean number of aphids per plant is displayed with the standard error, based on 30 repetitions, carried out each time with 20 aphids per experiment. (**): p value < 0.01, (***): p value < 0.001. HDB: Healthy Dessert Banana; HPB: Healthy Plantain Banana; IDB: Infected Dessert Banana; IPB: Infected Plantain Banana

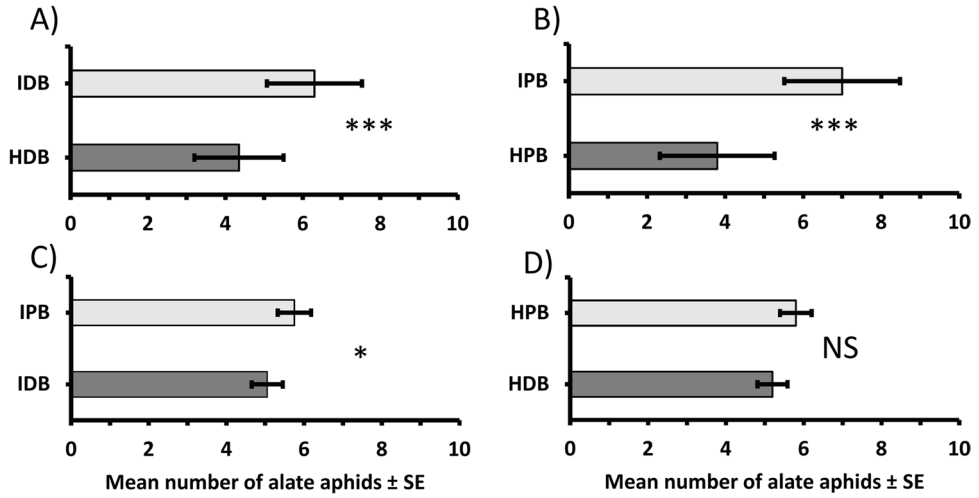

Fig. 2 Effect of banana plant treatment on the choice of alate aphids *P. nigronervosa*: **a** Healthy Dessert Banana and Infected Dessert Banana; **b** Healthy Plantain Banana and Infected Plantain Banana; **c** Infected Dessert Banana and Infected Plantain Banana; **d** Healthy Dessert Banana and Healthy Plantain Banana. The mean number of aphids per plant is displayed with the standard error, based on 20 repetitions, carried out each time with 20 aphids per experiment. NS: not significant, (*): p value < 0.05, (***): p value < 0.001. HDB: Healthy Dessert Banana; HPB: Healthy Plantain Banana; IDB: Infected Dessert Banana; IPB: Infected Plantain Banana

($F = 3.3$, $R^2 = 0.07$, $p = 0.02$). This means that for some VOCs, the effect of the virus differed between both varieties (permutational MANOVA, Fig. 3).

Considering only the VOCs common to the two genotypes, the plantains emitted the greatest amounts of VOCs, with the exception of three VOCs for the healthy bananas ((*Z*)-β-ocimene, 4,8-dimethyl-1,3,7-nonatriene and 6-methyl-3,5-heptadien-2-one) and five VOCs for infected bananas ((*Z*)-β-ocimene, 6-methyl-3,5-heptadien-2-one, methyl salicylate, myrcene, and nonanal) (Fig. 4). In

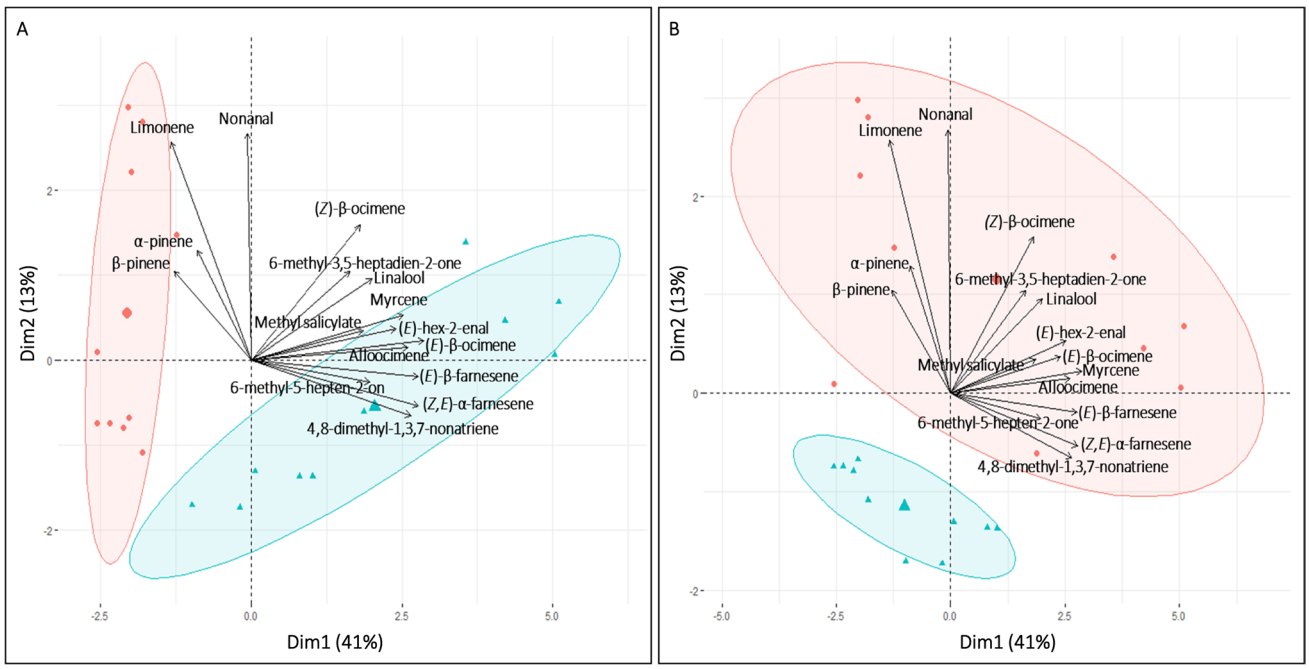

Fig. 3 Principal component analysis (PCA, supported by 41% inertia on the first axis, and 13% on the second axis) of the 16 selected VOCs emitted by banana plants. **a** Between the plantain (blue) and the dessert banana genotypes (red) considering both infection status (healthy and infected); **b** Between the healthy banana plants (blue) and the infected banana plants (red) considering both genotypes (plantain and dessert). Ellipses represent 95% confidence intervals formed around the barycenter of each group (big dot or triangle). Each small dot or triangle represents a replicate (i.e., a banana plant, N = 10)

Table 1 Statistical results (GLM negative binomial) of the effect of BBTV on quantities of VOCs emitted by different types of banana plants. Significant results ($p < 0.05$) are in bold. For each comparison (i.e., between genotypes or between infection status), the relative proportion (Rp) of VOC emission increase is given as a ratio of plantain/dessert or infected/healthy plants. For example, $Rp_{healthy}$ indicates 5.7 for myrcene, which means that this compound was emitted in 5.7 times higher quantity in healthy plantain banana plants than in healthy dessert banana plants. $Rp_{plantain}$ indicates 2.8 for myrcene, which means that this compound was emitted in 2.8 times higher quantities in infected plantain banana plants than in healthy plantain banana plants. Dashes indicate that the difference in VOC emission between two categories could not be calculated (e.g., if a given VOC is not emitted by one banana plant category). See Fig. 4 for a comparison of VOCs emitted from each type of banana plant

Variable	Genotype					Infection			Genotype * infection	
Molecule	Healthy	Infected	χ^2	p	Dessert	Plantain	χ^2	p	χ^2	p
	$Rp_{healthy}$	$Rp_{infected}$			$Rp_{dessert}$	$Rp_{plantain}$				
(E)-hex-2-enal(E)-hex-2-enal	72.2	3.0	55.5	<0.001	45.9	1.9	354	<0.001	25.3	<0.001
(E)-β-farnesene(E)-β-farnesene	-	-	0.001	**0.99**	-	2.4	9.8	**<0.01**	0.001	0.99
(E)-β-ocimene(E)-β-ocimene	13.6	8.9	149.4	**<0.001**	5.5	3.6	54.3	**<0.001**	1.5	0.22
(Z)-β-ocimene(Z)-β-ocimene	0.9	2.1	1.3	**0.23**	2.8	6.4	25.3	**<0.001**	1.9	0.15
(Z,E)-α-farnesene(Z,E)-α-farnesene	-	-	0.001	**0.99**	-	1.8	99	**<0.001**	0.001	0.99
4,8-Dimethyl-1,3,7-nonatriene	-	-	688.6	<0.001	-	1.7	3.5	**<0.05**	0.001	0.99
6-Methyl-3,5-heptadien-2-one	2.3	1.8	7.1	**<0.01**	2.8	2.3	12.1	**<0.001**	0.25	0.69
6-Methyl-5-hepten-2-one	1.3	1.6	3.3	**0.06**	1.4	1.8	0.5	**0.48**	1.3	0.26
Alloocimene	-	-	0.001	0.99	-	4.3	10.9	**<0.001**	0.001	**0.99**
Limonene	0.0	0.0	213.9	**<0.001**	5.4	-	11.6	**<0.001**	0.001	0.99
Linalool	3.3	2.3	16.1	<0.001	5.4	3.8	36.1	**<0.001**	0.5	0.48
Methyl salicylate	3.9	1.7	23.1	<0.001	3.5	1.5	17.4	**<0.001**	4.9	<0.05
Myrcene	5.7	3.1	10.5	**<0.01**	5.2	2.8	9.2	**<0.01**	0.5	**0.48**
Nonanal	84.2	0.7	5.6	**0.06**	1517.0	12.4	110.7	**<0.001**	34.7	<0.001
α-Pinene	0.0	0.1	17.6	**<0.001**	3.3	-	6.3	**<0.05**	0.001	**0.99**
β-Pinene	0.0	0.0	226.2	<0.001	8.5	-	37.5	**<0.001**	0.001	0.99

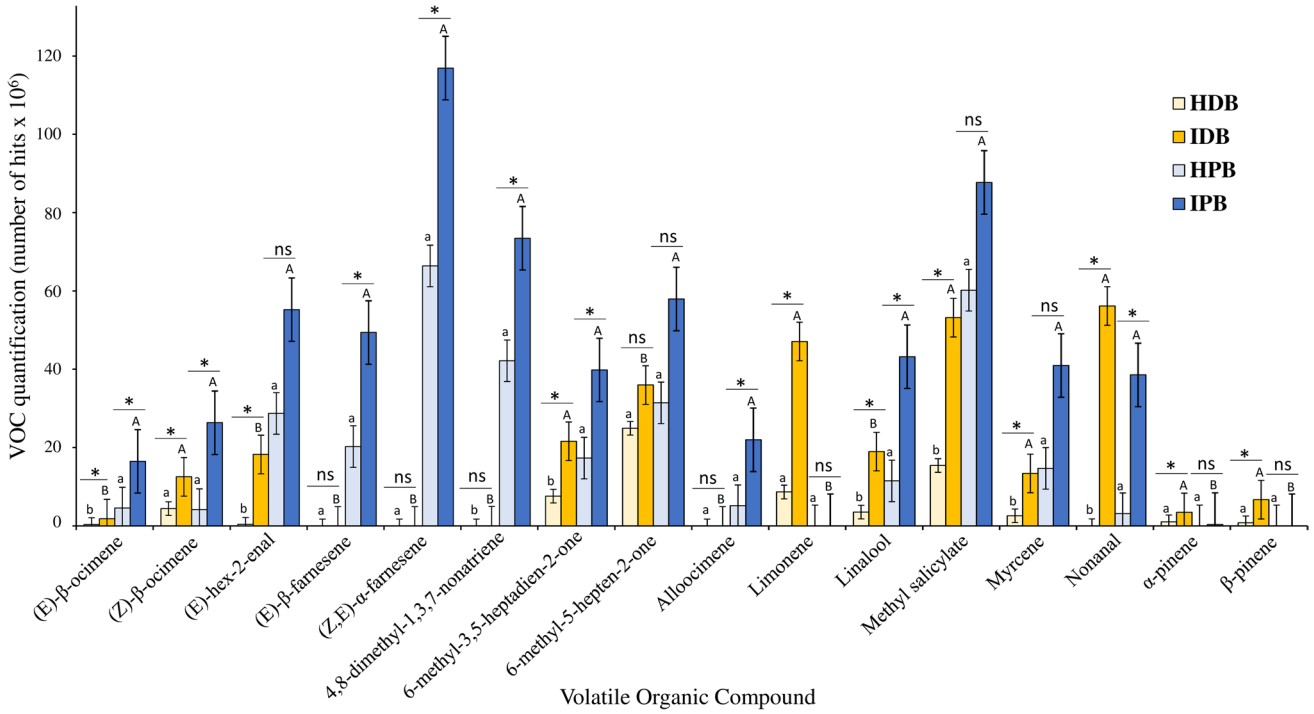

Fig. 4 Comparison of volatile organic compounds (VOCs) emitted by both genotypes (dessert: yellow, and plantain: blue), for both infection status by *Banana bunchy top virus* (BBTV; healthy banana: light color, and infected banana plant: dark color). The observed mean peak area (number of hits on the detector) with the standard error over five replicates are represented. Statistical results (GLMs): *ns* indicate non-significant results ($p > 0.05$), stars indicate significant differences ($p < 0.05$) between infection status (for each genotype), and different letters indicate significant differences ($p < 0.05$) between genotypes (for each infection status). HDB: Healthy Dessert Banana; HPB: Healthy Plantain Banana; IDB: Infected Dessert Banana; IPB: Infected Plantain Banana

addition, infected plants emitted greater amounts of VOCs than healthy plants, except one VOC for dessert banana (6-methyl-5-hepten-2-one) and four VOCs for plantain ((*E*)-hex-2-enal, 6-methyl-5-hepten-2-one, methyl salicylate, and myrcene), for which the viral infection did not modify the amount of VOC emitted (Fig. 4).

Overall, and still considering only the common VOCs, the banana plant genotype had a significant influence on the quantity of emitted VOCs, except for 6-methyl-5-hepten-2-one, (*Z*)-β-ocimene, and nonanal (Table 1). The infection with BBTV had a significant influence on VOC emissions from banana plants, except for 6-methyl-5-hepten-2-one. The genotype-infection interaction influenced only nonanal, methyl salicylate, and (*E*)-hex-2-enal (see Fig. 4).

Our results, therefore, reveal that the genotype acts on both the quality and the quantity of VOCs emitted by bananas plants, while infection by BBTV mainly acts on the increase in the VOC quantities.

Discussion

In this study, we observed that BBTV infected banana plants, regardless of the genotype, were more attractive for both apterous and alate *P. nigronervosa* aphids, which could lead to higher viral transmission. Plantain bananas were also more attractive than dessert ones, regardless of their BBTV infection status. This matched with our observation that plantains produced greater quantities of VOCs. We also found that infected plants released similar VOC profiles as healthy plants but in much greater quantities. These differences may explain the greater attraction of *P. nigronervosa* towards infected bananas. At this stage, however, it is difficult to determine whether this difference is linked to a physiological effect of the virus on the plant or a real manipulation by the virus, aimed at making the plant more attractive for aphids to increase its transmission (Chesnais et al. 2019a).

Indeed, it is known that various phytoviruses transmitted by aphids directly influence VOC emission and indirectly

the patterns of attraction, retention, performance, and dispersion of vectors (Belliure et al. 2005; Bosque-Pérez and Eigenbrode 2011; Carmo-Sousa et al. 2014; Eigenbrode et al. 2018; Mauck et al. 2010; Shapiro et al. 2012; Tungadi et al. 2017). By such phenotypic changes, the virus can manipulate the vector through the plant (Eigenbrode et al. 2018; Thomas et al. 2005), and favors its propagation and epidemiological dynamics (Ingwell et al. 2012; Sisterson 2008). Our results are similar to those reported by Jimenez-Martinez et al. (2004), who showed that the cereal aphid *R. padi* was more attracted by wheat plants infected with *Barley Yellow Dwarf Virus* (BYDV) than by healthy plants. The attraction preference of aphids to the plantain variety could be due to the higher amounts of VOCs emitted by this genotype, regardless of the infection status of the plant. The Cavendish dessert genotype is a strict triploid (AAA) belonging to the species *M. acuminata*, whereas the plantain is a triploid hybrid (AAB) belonging to the species *M. paradisiaca* and derived from the cross *M. acuminata* x *M. balbisiana* (Simmonds 1962). This genotypic demarcation between Cavendish and Pacific plantain underlies differences in their metabolic profiles, such as VOCs, involved in the short distance communication between insects and their environments (Bernasconi et al. 1998; Piesik et al. 2013).

Our results with infected banana are consistent with those of Chesnais et al. (2019b), who observed that the aphid *My. persicae* prefers to settle and feed on the wild genotype of camelina (*Camelina microcarpa*) infected by but tolerant to *Turnip Yellows Virus* (TuYV), than on the cultivated genotype (*C. sativa*) and their F1 hybrid, consequently increasing the number of viruliferous aphids. In our study, *P. nigronervosa* preferred to settle on infected plantain (apparently, less susceptible to BBTV), compared to more susceptible Cavendish dessert banana (Hooks et al. 2009; Su et al. 1992). Indeed, dessert bananas are subject to many diseases because of their narrow genetic basis (Abadie et al. 2003).

According to Eigenbrode et al. (2018), persistently transmitted viruses more frequently attract their vectors and improve their performance on infected plants compared to viruses with non-persistent transmission. Indeed, for persistent transmission, which is the case for BBTV, the viral vector is likely to develop a strong affinity with the host plant. The reason is that the acquisition of the virus requires sustained feeding in the phloem of the infected plant (four hours minimum for BBTV), the time for the virus to circulate inside the insect to the salivary glands where the virions reside. In that case, the aphid infectivity can last a long time, often even until his death as for *P. nigronervosa* (Fereres and Raccah 2015; Gray et al. 2014; Lepoivre 2003; Raccah and Fereres 2009). This is not the case for non- (or semi-) persistent viruses, such as CMV, where the vector appears to be falsely attracted to the infected plant, and then disperses rapidly (Mauck et al. 2010; Tungadi et al. 2017). The vector immediately transmits the virus after a very short acquisition time, from a few seconds to a few minutes (Harris et al. 1977). To optimize its transmission and propagation, the non-persistent virus induces a pull–push strategy from its vector to its host plant (Carmo-Sousa et al. 2014). This shows that vector manipulation traits appear to be adaptive depending on the virus transmission mechanism (Mauck et al. 2012, 2018; Mauck and Chesnais 2020).

We compared the attractiveness responses of two *P. nigronervosa* forms (apterous and alate) to banana plants, comparing the four plant treatments. We found that both aphid forms were attracted to banana plants in similar ways, even though the apterous aphids are reputed to be less sensitive to odors because they have fewer sensorial organs, such as rhinaria (Hullé et al. 1999; Yongjun et al. 1995). However, in the "healthy dessert banana (HDB)—healthy plantain banana (HPB)" test, apterous aphids were significantly more attracted to the HPB, while the alate aphids were attracted similarly to HDB and HPB. The two forms of aphids were not confronted with the same signals, because the apterous aphids were tested in a Y-tube olfactometer whereas the alates were tested in settling cages. For the alates, other signals resulting from the putative manipulation, such as color, size, texture, metabolites in the leaves, tusks, and cuticles of the leaves, may have been involved in the orientation of the vectors (Mauck and Chesnais 2020).

We showed a clear discrimination between two groups of treatments (infected vs. healthy, and plantain vs. dessert) based on the overall set of detected VOCs. In the genotypic comparison, the discrimination of banana plants was mostly driven by the compounds that are specific to each genotype, in addition to differences in emitted quantities. In the infection status comparison, the discrimination was driven by the overall differences in emitted quantities of VOCs, but not by differences in the nature of emitted VOCs. Infected bananas emitted the greatest amounts of VOCs (at the exception of 6-methyl-3,5-heptadien-2-one), regardless of their genotype, which once again suggests an effect of the viral infection on the phenotype of banana plants. For example, in tobacco (*Nicotiana tabacum* Cv. Ky 57), the infection by a virus leads to an increase in the synthesis of ethylene (Chaudhry et al. 1998), a volatile phytohormone acting in synergy with other volatile emitted by plants (Ruther and Kleier 2005). It seems obvious that most of the VOCs potentially involved in the attractiveness of *P. nigronervosa* are found among the nine common VOCs identified in this work ((*E*)-hex-2-enal, (E)-β-ocimene, (Z)-β-ocimene, 6-methyl-3,5-heptadien-2-one, 6-methyl-5-hepten-2-one, linalool, methyl salicylate, myrcene, and nonanal).

Berhal et al. (2017) identified 11 VOCs from healthy Cavendish and 13 VOCs from healthy Pacific plantain banana plants. We found that 6 VOCs (6-methyl-5-hepten-2-one,

myrcene, (*Z*)-β-ocimene, (*E*)-β-ocimene, methyl salicylate, and 6-methyl-3,5-heptadien-2-one) were common between our study and theirs. Nonanal was not identified in the study by Berhal et al. (2017), while we did not find β-ionone and (*E, E*)-α-farnesene. The principal component analysis shows that nonanal plays a role in distinguishing infected bananas from healthy bananas, being more concentrated in virus-infected plantain and dessert bananas. This compound marks the greatest difference between healthy and virus-infected plants for the two varieties. In the future, more attention will be paid to this compound to test its attractivity, and if the virus favors its emission.

All of these VOCs are known to play a role in plant–insect interactions and insect control (pherobase.com; Stenberg et al. 2015). Some of them (α-pinene, β-pinene, limonene, myrcene, (*E*)-β-farnesene, ocimene, and linalool) are insect repellents (Arimura et al. 2004; Byers et al. 1979; Francis et al. 2005; Lípez et al. 2011; Smith 1965; Xu et al. 2018), whereas others (methyl salicylate) are especially attractive to natural enemies of aphids (James 2003; James and Price 2004; Xu et al. 2018). Other volatiles, in particular nonanal and (*E*)-hex-2-enal, are known to be attractive to various taxa, including phytophagous insects and natural enemies (predators and parasitoids) (Allmann and Baldwin 2010; Halitschke et al. 2008, Hoballah and Turlings 2005; Syed and Leal 2009; Xu et al. 2020). In general, the same VOCs can be attractive and repellent, depending on their emission rate. This is the case, for example, for (*E*)-β-farnesene, which is an alarm pheromone in aphids (Francis et al. 2005), but can act at very low concentrations as an aggregation pheromone, providing information on the quality of the host plant (Verheggen et al. 2009). In addition, some studies on insect behavior suggest that the composition of the mixture of volatile plants is crucial and that specific mixtures are more attractive than individual compounds (Visser et al. 1996; Natale et al. 2003; Toby et al. 2005). In our study, we suggest that the differences in attraction of *P. nigronervosa* between the two genotypes are due to both quantitative and qualitative variations in the VOCs emitted (i.e., a potential mixture effect), while between the two infection statuses, it is due to variability in the quantities emitted.

Conclusion

This study highlights the role of the differential composition and relative proportions of VOCs on the attractiveness of alate and apterous *P. nigronervosa* for infected or healthy dessert or plantain banana plants. Identification of volatile compounds revealed a total of 16 VOCs (12 for dessert banana and 13 for plantain), with the highest emission in plantains and in infected banana plants. The compounds which seem potentially involved in the attractiveness of aphids to banana plants are (*E*)-hex-2-enal, (*E*)-β-ocimene, (*Z*)-β-ocimene, (*E*)-β-farnesene, 6-methyl-5-hepten-2-one, methyl salicylate, myrcene, and nonanal. By modifying VOC emission by the plant, the virus may produce conditions that favor its propagation. It remains to be determined whether the fitness of the aphid vectors could also be affected by the viral infection. The next step would be to determine which of these common compounds, or mixtures thereof, can be used in the semiochemical control of *P. nigronervosa* as part of an integrated management approach. To do so, it would be important to test the application of these compounds in field conditions and to extend the studies on several varieties of banana plants.

Consent for publication

All coauthors consent for publication.

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Authors' contributions IMS performed the experiments and wrote a first draft of the manuscript. IMS and KT analysed data. TH secured funding and supervised the project. All coauthors significantly contributed to the realization of the study and in the revision of the manuscript.

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Declarations

Conflict of interest None.

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