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PEST MANAGEMENT

Repellency of Wild Oregano Plant Volatiles, *Plectranthus Amboinicus*, and Their Essential Oils to the Silverleaf Whitefly, *Bemisia Tabaci*, on Tomato

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Abstract

The *Bemisia tabaci* (Gennadius) whitefly is a major economically damaging pest of many crops such as tomato (*Solanum lycopersicum* L.). Pesticides are widely used to control *B. tabaci* while the use of aromatic plants is an alternative control method. The aim of this study was to assess the *B.tabaci* repellent effect of wild oregano, *Plectranthus amboinicus* (Lour.) Spreng, a widespread aromatic plant in the West Indies. We tested three origins of wild oregano, including northern, central, and southern Martinique (French West Indies). Our results showed that all essential oils of wild oregano had either masking properties or were true repellents—the mean percentage of whiteflies present in the upper part of the still-air olfactometer was 1.3- to 1.9-fold lower than in the controls. The ethanolic solution of volatile organic compounds of wild oregano from southern Martinique also had a true repellent effect—the mean percentage of whiteflies present in the upper part of the still-air olfactometer was 1.3-fold lower than in the controls. Moreover, in a greenhouse insect-proof cage, there were 1.5 fewer adult whiteflies on tomato intercropped with wild oregano from southern Martinique than on tomato alone after 96 h exposure. Our study generated further insight into the potential of *P. amboinicus* for *B. tabaci* biocontrol on tomato crops. Wild oregano extracts were repellent to *B. tabaci* and could be used as a companion plant to prevent whitefly infestations on tomato crops. However, the *B. tabaci* behavior depends on the plant origin.

Keywords *Coleus amboinicus* · essential oils · volatile organic compound · intercropping · plant-insect interactions · pest management

Introduction

Aromatic plants are commonly used as companion plants in pest management programs. Companion planting is a specific polyculture method in which two plant species are supposed to synergistically improve one and other's development (Parker et al. 2013). Some companion plants are used to enhance biological pest control by providing habitat (e.g., insectarium plant) or food sources (e.g., pollen and nectar) for natural enemies. Yet some aromatic plants specifically target the pest. Aromatic plants are also sometimes used in their extract form (e.g., essential oils) for pest management (Isman 2005). Many studies on pest management study the repellent activity of aromatic plants used as companion plants, essential oils (EOs), or other extract forms (Deletre et al. 2016; Campos et al. 2019; Isman 2020). When used as repellents, aromatic plants, i.e., intercrops or extracts, serve to prevent and disrupt host location via chemical stimuli. Herbivore insects select their host plants based on visual and chemical cues for feeding and/or selecting oviposition sites (Visser 1983). Herbivores thereby receive and analyze olfactory cues, i.e., plant-emitted volatile organic compounds (VOCs), to recognize their host and non-host plants (Cunningham 2012). A plant or its extract can be attractant, non-attractant, or repellent for herbivores depending on the emitted VOCs (Szendrei and Rodriguez-Saona

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2010; Bruce and Pickett 2011). Deletre et al. (2016) defined different repellence phenomena, including true repellent effects whereby insect movements are channeled away from the odor source, which is the function of repellent aromatic plants. The odor masking effect is another repellence phenomenon which involves interference with the mechanisms whereby insects recognize host plants by decreasing or inhibiting its attractiveness toward the host plant, and masking aromatic plants fall into this category. It is essential to study types of repellency phenomena to control pests, especially when the polyphagous nature of pests complicates their management via traditional methods. Whiteflies have several sensilla with an olfactory function so they can discriminate numerous VOCs and are affected by the odor confusion (Mellor and Anderson 1995; Schlaeger et al. 2018).

The whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) is a major worldwide polyphagous pest that can damage over 500 crop species such as tomato (*Solanum lycopersicum* L.), tobacco (*Nicotiana tabacum* L.), and cotton (*Gossypium hirsutum* L.), often with a heavy economic impact (Ying et al. 2003; Ryckewaert and Rhino 2017). Whiteflies damage crops directly by feeding on the leaves, or indirectly by (i) the development of sooty mold on *B. tabaci* honeydew and (ii) the transmission of more than 100 viruses to the crops, including the tomato yellow leaf curled virus (TYLCV) that can devastate tomato crops (Moriones and Navas-Castillo 2000; Jones 2003). Pesticides are widely used to control *B. tabaci* but pests tend to become pesticide-resistant in the long term and chemical management is harmful to humans and the environment (Gorman et al. 2010; Palumbo et al. 2001; Horowitz et al. 2020). Efficient alternative methods are thus urgently needed to manage *B. tabaci*.

Making effective use of aromatic plants represents an alternative *B. tabaci* control method. Tomatoes associated with coriander (*Coriandrum sativum* L.) were less infested by *B. tabaci* than tomatoes alone (Togni et al. 2010). A reduction in *B. tabaci* infestation was also found in tomato fields intercropped with Greek basil (*Ocimum basilicum* L.) (Carvalho et al. 2017). Many aromatic plant EOs are repellent to *B. tabaci*, including winter savory (*Satureja montana* L.) (Deletre et al. 2015).

Wild oregano (WO), *Plectranthus amboinicus* (Lour.) Spreng, also known as *Coleus amboinicus* Lour. or *Coleus aromaticus* Benth., is a perennial tropical aromatic plant. This succulent plant is traditionally used in Martinique (French West Indies) and throughout the Caribbean region. WO is used as a spice and for its medicinal properties (Lukhoba et al. 2006). WO is also used as a companion plant or extract in pest management strategies. Calumpang (2013) demonstrated that the population of cutworm *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae) was reduced on eggplant (*Solanum melongena* L.) associated with WO. Besides, EOs collected from WO can also be used in pest management against cowpea bruchid *Callosobruchus maculatus* (Fabricius) (Coleoptera: Chrysomelidae) (Wanna and Kwang-Ngoen 2019). EO of another plant of the same genus as WO, *Plectranthus neochilus* (Schltr.), also has repulsive effects against *B. tabaci* (Fanela et al. 2016). Studies have shown that WO have two chemotypes, i.e., carvacrol and thymol, depending on the geographic origin (Arumugam et al. 2016; Hsu and Ho 2019). The difference in chemotypes within the same species can be the result of biotic (pollination, phonologic cycle, etc.) or abiotic (season, soil type, etc.) factors (Peñuelas and Llusià 2001). In Martinique, carvacrol is the main compound of WO (Prudent et al. 1995). We thus hypothesized that, as a plant extract or companion plant, *P. amboinicus* with a carvacrol chemotype would have a repellent effect on *B. tabaci*. Winter savory (WS) EO with carvacrol as main volatile compound was found to be repellent to *B. tabaci* (Deletre et al. 2015), as also were carvacrol lures placed in on the tops of tomato plants (Lee et al. 2019). WO has yet to be studied in detail as a repellent plant for *B. tabaci* control. This study was designed to assess the repellent effects of different natural WO extracts on *B. tabaci* in olfactometry bioassays, as well as the effectiveness of intercropping WO plants with tomato plants in greenhouse conditions.

Materials and methods

Study site

This study was conducted at the CIRAD French West Indies research site in CAEC, Le Lamentin, Martinique. The area has a humid tropical climate with 2094 mm yearly average rainfall and an average daily temperature of 23.3–30.2°C.

Plants

Determinate tomato variety "Heat Master" (Seminis seeds) plants were used for the experiments. They were bought at a local nursery and kept in a greenhouse without pesticide application. The plants were used at the six–true leaf stage for olfactometry bioassays and the ten–true leaf stage for greenhouse bioassays.

WO mother plants were collected from three sites with different pedoclimatic characteristics (Table 1) to take into account the variability of the chemical profiles of essential oils produced (Zouari (2013). They were then propagated by cuttings and cultivated in a commercial plotting soil (Plantaflor) in a greenhouse nursery. After 4 weeks, some WO plants were transplanted in bigger pots (2 L) filled with soil (Nitisol) from the CIRAD research station. They were then kept outside under natural climatic conditions

Table 1 Description weather and soil type of the three wild oregano locations

Wild oregano code	Locality	Annual average temperature (°C)	Annual rainfall (mm)	Type of soil
WO1	Bellefontaine (North-Caribbean)	23.1–29.1	2020.5	Vertisol
WO2	Le François (Center-Atlantic)	23.8–32.0	1562.9	Nitisol
WO3	Ste-Anne (South)	23.9–29.8	1550.1	Vertisol

for later use in the ethanolic VOC solution-making process. Other WO plants were cultivated in open field to produce essential oils.

Plant extracts

Essential oils

*P. amboinicu*s EOs were made by turbodistillation at the *Pôle Agroressouces et de Recherche de Martinique* (PARM). EOs were analyzed with a gas chromatograph (Varian 450 GC) equipped with a DB5 MS non-polar capillary column (30 m × 0.25 mm × 0.25 µm, Agilent Technologies) coupled with a mass spectrometer (Varian 240-MS Ion Trap) operating in full scan mode with a 35 to 350 m/z range. Each sample was a solution of EO diluted with acetone at 2% (w/w) concentration. One microliter of sample was injected in split mode at 1:100 ratio. The injector temperature was set at 250°C, and the oven temperature was initially at 55°C then programmed to 195°C at the rate of 7°C/min. Helium was used as a carrier gas with a 1.0 mL/min flow rate. The tentative identification of the compounds was based on the matching of spectra with those in the NIST Library (NIST08), and on *P. amboinicus* volatiles already identified in the literature (Arumugam et al. 2016; Hsu and Ho 2019; Prudent et al. 1995).

We also used *S. montana* EO (Phytosun Arôms), also called winter savory (WS). The percentage of EO and VOCs compounds was calculated from the peak areas integrated in the analysis program.

Ethanolic VOC solutions of *P. amboinicus*

Dynamic headspace trappings were obtained from randomly chosen plants. VOCs of *P. amboinicu*s plants cultivated in outdoor pots were collected for 24 h. Whole plants were enclosed in an odorless Nalophan bag and air was drawn through a HayeSep Q volatile trap using an automated portable VOC collection system (Volatile Assay Systems, Rensselaer, NY). The VOCs of each plant were then eluted with 200 µL of pure ethanol, and VOCs of 15 WO plants per origin were collected.

Insects

The *B. tabaci* whitefly population was collected in a melon field in southern Martinique (14°26′21″N, 60°52′44″W) and kept in rearing cages on tomato plants in a climate room at 26±1°C, 45% RH under a 12:12 photoperiod before use in the olfactometric tests. Insects were collected four times the first month to start the population, and then once every 2 months to maintain the population. Whiteflies of mixed age and sex were used in the bioassay.

Olfactometric bioassay

Olfactometer design

The same still-air olfactometer (Legallais, Montpellier, France) described by Deletre et al. (2015) was used. The olfactometer was composed of a glass cylinder (L: 30 cm, ø: 3 cm) closed at the top with a stopper and another stopper part, pierced with a smaller cylinder (L: 10 cm, ø: 0.5 cm) at the bottom. The olfactometer was vertically exposed to white light (50 W, 350 lm, 4000 K "cool white," Parathom LED (OSRAM)), so as to prompt the whiteflies to naturally fly upwards because of their positive phototaxis. (i) Discs (ø 2.5 cm) of sterilized filter paper or (ii) tomato leaflets were treated with 60 µL of the solutions described in the following paragraphs. They were then dried for 1 min under a fume hood and placed at the top end of vertical cylinder (Zhang et al. 2004). After 80 s in the freezer at −25°C, 10 to 15 whiteflies were introduced in the lower part. After 1 h, we recorded the number of whiteflies in the upper part from 0 to 2 cm from the top, and in the lower part. For both experiments, there were 15 replications per tested modality, one olfactometer per replication. Our system consisted of a set of nine individual olfactometers numbered from one to nine. For each set, we tested up to 7 modalities at the same time as two control olfactometers. One of the control olfactometers was empty (without any tested material in it, called "air") and served as a whitefly activity control. The other control olfactometer had filter paper or tomato leaflet treated with 60 µL of pure ethanol. Applying the solution on filter papers allowed us to evaluate the true repellency effect because only EO or ethanolic VOC solution odors were circulating within the olfactometer. The test solution and tomato odor were combined by applying the solution on a tomato leaflet, thereby enabling us to assess the masking effect.

Behavioral response of *B. tabaci* to *P. amboinicus* essential oils

The effect of *P. amboinicus* EO on whiteflies behavior was studied according to the method of Zhang et al. (2004). *Satureja montana* EO was used as reference repellent EO because it is repellent against *B. tabaci* and its major compound is also carvacrol (Deletre et al. 2015). EOs were diluted in ethanol at three mass concentrations 833, 1666, and 3333 µg/mL. Sixty microliters of solution was applied on filter paper disc or tomato leaflet disc i.e., 50, 100, and 200 ng of EO per disc.

Behavioral response of *B. tabaci* to ethanolic VOC solution of *P. amboinicus*

The effect of the *P. amboinicus* ethanolic VOC solution on whitefly behavior was studied using the method described above. Sixty microliters of ethanolic VOC solution was applied on filter paper discs or tomato leaflets discs.

Greenhouse tests

The experiment was conducted in an insect-proof cage with a 60 m^2 surface area in a greenhouse. Four modalities were studied: (i) tomato alone, (ii) tomato with WO1, (iii) tomato with WO2, and (iv) tomato with WO3. Each test consisted of four growing trays with a surface area of 1.3 m^2 and soil volume of 0.18 m^3. The trays contained nine tomato plants alone or nine tomato plants with nine WO plants (Fig. 1). The greenhouse tests were repeated six times with different plants and the modalities were randomized in each case. For each test, 150 to 300 wild whiteflies collected in a melon field were released on the same day. *B. tabaci* adults were recorded on the tomato plants at three times, i.e., 3 h, 24 h, and 96 h after release. At the last time, the first three tomato leaves were collected, and the number of *B. tabaci* eggs was counted in the laboratory under a stereoscopic microscope.

Data analysis

To assess the repellent effect, we compared the proportion of whiteflies in the upper part of the olfactometer cylinders between treatments and controls (filter paper disc or tomato leaflet treated with pure ethanol and empty tubes) using a GLMM with binomial family with set and olfactometer

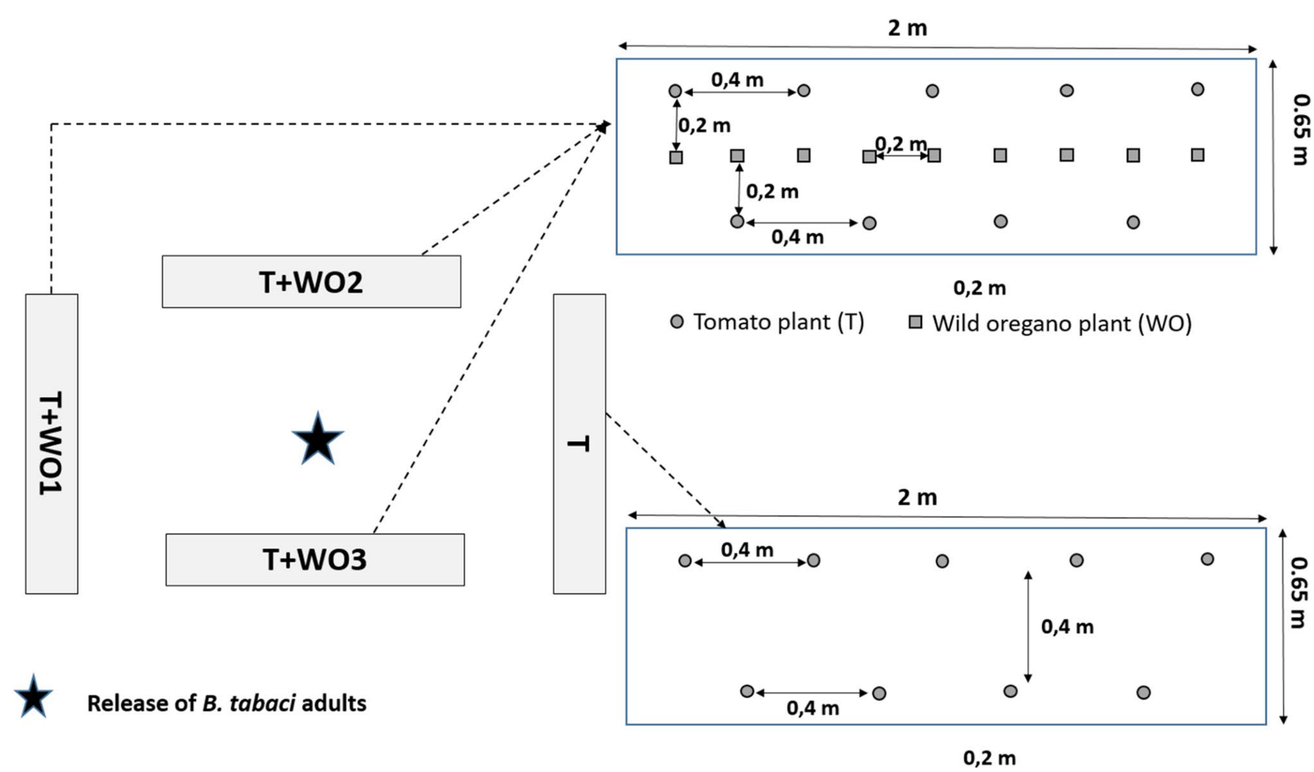

Fig. 1 Design of greenhouse test in an insect-proof cage with growing trays

within the set as random factors, followed by a Tukey post hoc test with $p < 0.05$ significance level.

For the greenhouse tests, we compared the distribution of *B. tabaci* adults and egg laying between tomato alone and different associations using a GLMM with Poisson distribution with replication as random factor as well as tray because data were paired. Pairwise comparisons were then done using a Tukey post hoc test with $p < 0.05$ significance level. All statistical analyses were done using R software version 3.6.1 (R Core Team 2019) with the lme4 (version 1.1-21) and emmeans (version 1.3.5.1) packages (Bates et al. 2015; Lenth 2019).

Results

Plant extracts analysis

We identified 14 compounds in WO extracts and 16 compounds in *S. montana* EO (Table 2; Figs. S1 and S2). Carvacrol and p-cymene were the main compounds in all WO extracts. β-caryophyllene was important in WO EO whereas its percentage is low in ethanolic VOC solutions. The main *S. montana* EO compounds were carvacrol, p-cymene, and γ-terpinene, in decreasing order.

Olfactometric bioassay

Behavioral response of *B. tabaci* to essential oils

The whitefly distributions differed in the control olfactometers and in those with EOs according to the concentrations, both for EOs applied to the filters (GLMM: Chisq = 94.51, df = 13, $p < 0.001$) and those applied to the tomato leaves (GLMM: Chisq = 133.81, df = 13, $p < 0.001$).

Figure 2 shows that WO2, WO3, and WS EOs had a repellent effect at specific concentrations. When WO2 EO was applied on filter paper discs at 100 and 200 ng/disc as well as when WO3 was applied at 200 ng/disc, the mean percentages of whiteflies present in the upper part of the olfactometer were 1.5-fold lower than in the control olfactometers. When WS EO was applied on filter paper discs at 50 and 100 ng/disc, the mean percentages of whiteflies present in the upper part of the olfactometer were at least 1.4-fold lower than in the control olfactometers.

Figure 3 shows that all tested EOs had a masking effect at specific concentrations. When WO2 EO was applied on tomato leaflet discs at all three concentrations, the mean percentages of whiteflies present in the upper part of the olfactometer were 1.4- to 1.7-fold lower than in the olfactometer with tomato leaflets alone. However, the results obtained when WO2 EO was applied at 100 and 200 ng/disc confirmed the true repellent effect, i.e., WO2 EO had a masking effect only at 50 ng/disc. At 100 ng/disc, when WO3 and WO1 EOs were applied on tomato leaflet discs, the mean percentages of whiteflies present in the upper part of the olfactometer were respectively 1.5- and 1.7-fold lower

Table 2 Percentage composition of essential oil and ethanolic VOC solution of wild oregano from different origins [northern (WO1), central (WO2), and southern (WO3) Martinique (French Indies)] and essential oil of winter savory (WS)

	Compounds	Essential oil				Ethanolic VOC solution		
		WO1	WO2	WO3	WS	WO1	WO2	WO3
1	α-Thujene	0.31	0.37	0.60	1.85	0.39	0.26	0.50
2	α-Pinene	0.13	0.16	0.30	1.50	0.22	0.79	0.48
3	1-Octen-3-ol	0.74	0.98	0.92	0.82	-	-	-
4	(−)-β-Pinene	0.64	0.92	1.17	2.12	0.64	0.43	1.03
5	α-Terpinene	0.92	1.54	1.71	3.15	0.55	-	0.81
6	p-Cymene	17.42	18.51	19.98	20.21	37.57	23.02	17.61
7	γ-Terpinene	5.11	8.68	9.21	14.03	3.12	1.80	3.94
8	Linalool	-	-	-	1.26	-	-	-
9	Borneol	-	-	-	1.51	-	-	-
9	Terpinen 4-ol	1.20	1.21	1.22	0.77	0.50	0.32	0.29
11	Carvacrol	40.47	36.96	36.98	38.56	41.77	50.13	58.02
12	β-Caryophyllene	12.91	13.12	12.02	2.41	1.58	1.12	2.30
13	trans-α-Bergamotene	9.53	8.02	7.04	0.15	1.69	1.33	1.88
14	α-Humulene	3.93	3.95	3.28	0.08	0.59	0.20	1.16
15	β-Bisabolene	0.58	0.44	0.35	1.35	-	-	-
16	Caryophyllene oxide	1.75	1.24	1.14	0.31	0.80	1.90	0.71

(-) not detected

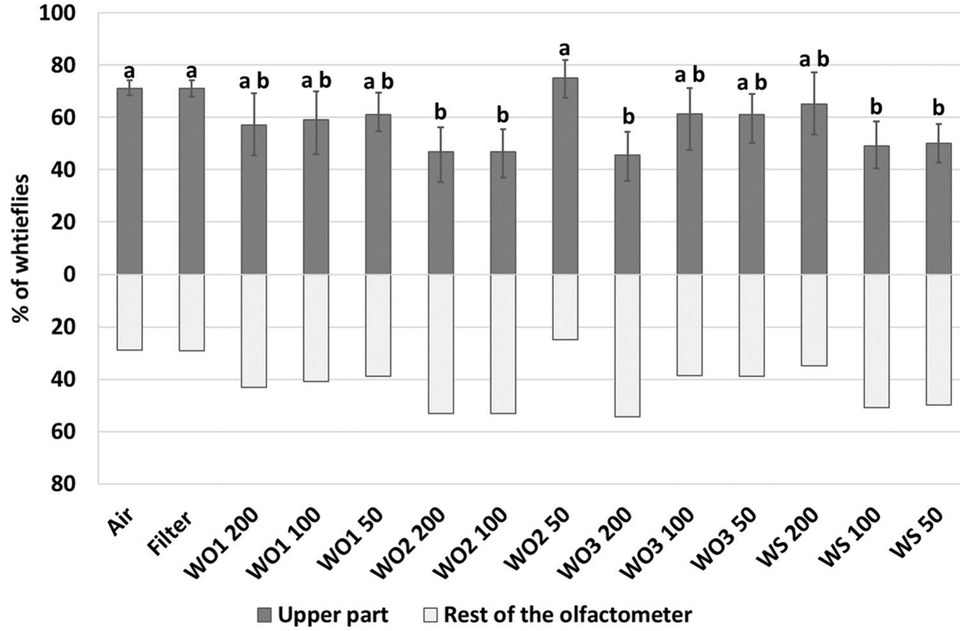

Fig. 2 Mean percentage (± IC) of whiteflies counted in the upper part (grey) and the rest of the olfactometer (white) 1 h after release in the olfactometer, in response to filter discs treated with various doses of wild oregano (WO) and winter savory (WS) essential oils and controls (empty tube=air/filter + ethanol = filter). Concentrations: 50, 100, and 200 ng in 60 µL of pure ethanol. Wild oregano origins: WO1 (north), WO2 (center), WO3 (south). Means are labeled by different letters (a, b) significantly different from each other (Tukey post doc test, $p \leq 0.05$)

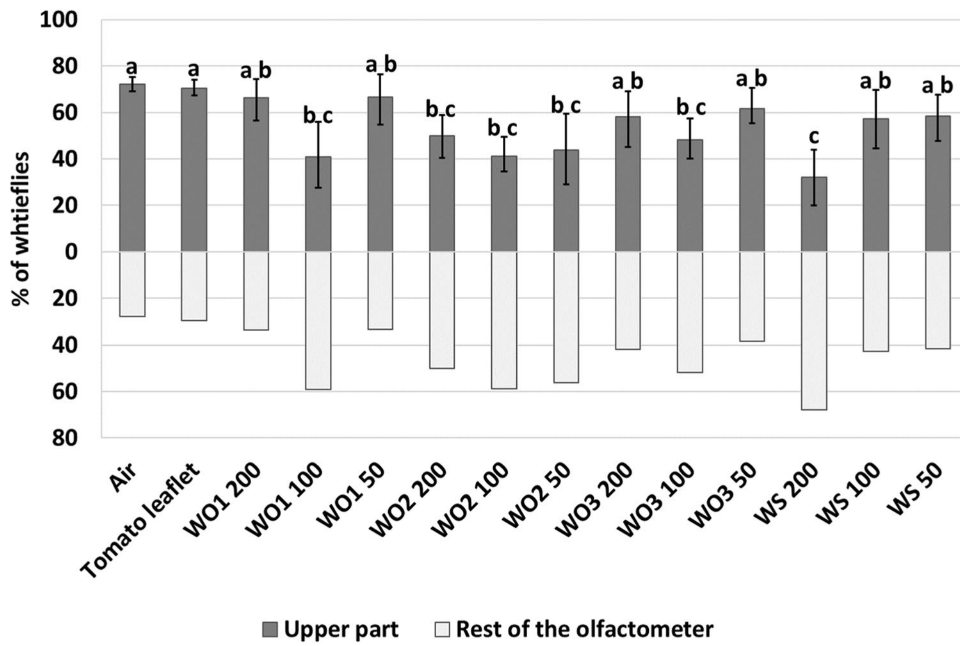

Fig. 3 Mean percentage (± IC) of whiteflies counted in the upper part (grey) and the rest of the olfactometer (white) 1 h after release in the olfactometer, in response to tomato leaflet discs treated with various doses of wild oregano (WO) and winter savory (WS) essential oils and controls (empty tube=air/tomato leaflet + ethanol = tomato leaflet). Concentrations: 50, 100, and 200 ng in 60 µL of pure ethanol. Wild oregano origins: WO1 (north), WO2 (center), WO3 (south). Means are labeled by different letters (a, b, c) significantly different from each other (Tukey post doc test, $p \leq 0.05$)

than in the olfactometer with tomato leaflets alone. When WS EO was applied on tomato leaflet discs at 200 ng/disc, the mean percentage of whiteflies present in the upper part of the olfactometer was 1.8-fold lower than in the olfactometer with tomato leaflets alone.

Behavioral response of *B. tabac*i to ethanolic VOC solution of *P. amboinicus*

The whitefly distributions within the olfactometer significantly differed between controls and WO ethanolic VOC solutions, both for those applied to the filter (GLMM: Chisq = 21.38, df = 4, $p < 0.001$) and those applied to the tomato leaflets (GLMM: Chisq = 44.48, df = 4, $p < 0.001$).

The WO3 ethanolic VOC solution had a repellent effect (Fig. 4). When applied on filter paper discs, the mean percentage of whiteflies present in the upper part of olfactometer was 1.3-fold lower than in the control olfactometers.

WO1 and WO2 ethanolic VOC solutions had a masking effect (Fig. 5). When they were applied on tomato leaflet discs, the mean percentages of whiteflies present in the upper part of olfactometer were respectively 1.3- and

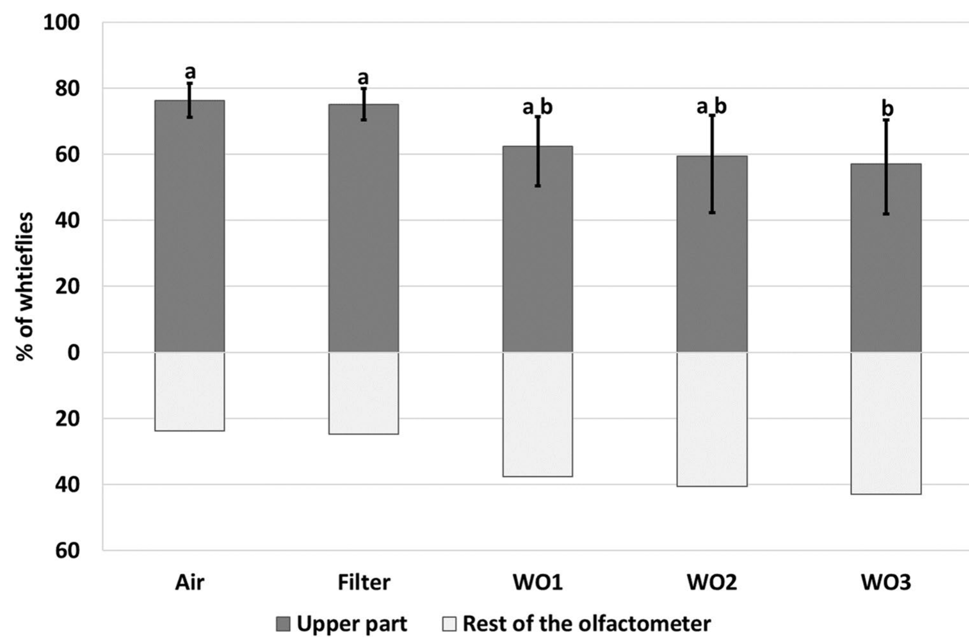

Fig. 4 Mean percentage (± IC) of whiteflies counted in the upper part (grey) and the rest of the olfactometer (white) 1 h after release in the olfactometer in response to filter discs treated with 60 µL of ethanolic VOC solution of wild oregano and controls (empty tube=air/filter + ethanol = filter). Wild oregano origins: WO1 (north), WO2 (center), WO3 (south). Means are labeled by different letters (a, b, c) significantly different from each other (Tukey post doc test, $p \leq 0.05$)

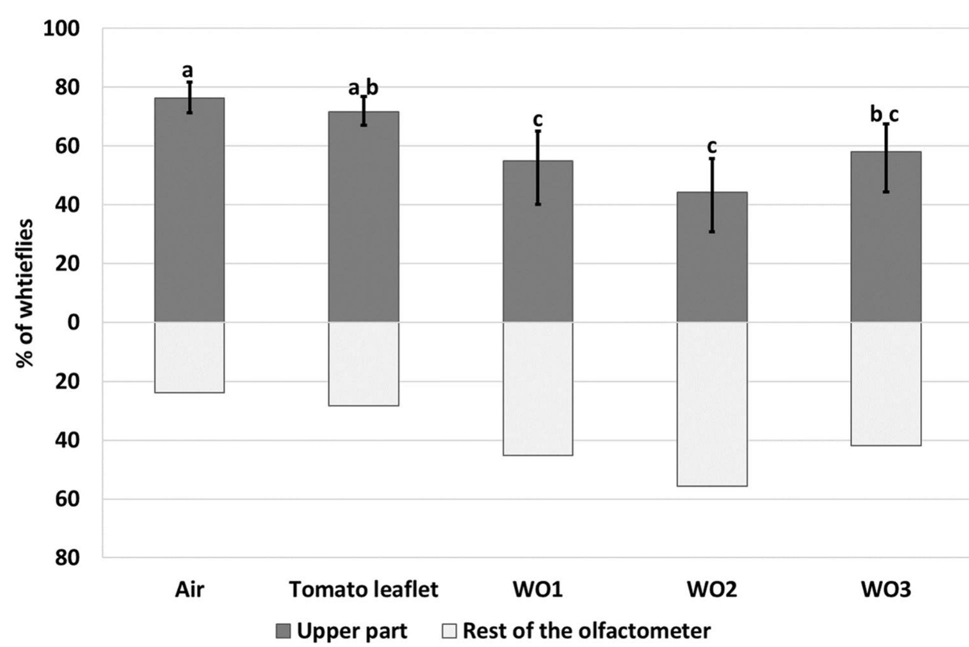

Fig. 5 Mean percentage (± IC) of whiteflies counted in the upper part (grey) and the rest of the olfactometer (white) 1 h after release in the olfactometer in response to tomato leaflet discs treated with 60 µL of ethanolic VOC solution of wild oregano and controls (empty tube=air/tomato leaflet + ethanol = tomato leaflet). Wild oregano origins: WO1 (north), WO2 (center), WO3 (south). Means are labeled by different letters (a, b, c) significantly different from each other (Tukey post doc test, $p \leq 0.05$)

1.6-fold lower than in the olfactometer with tomato leaflets alone.

Greenhouse tests

The *B. tabaci* adult population distribution varied between the different tomato and WO set ups after 3 h (Chisq = 27.58; df=3; $p = < 0.001$), 24 h (Chisq = 10.6; df=3; $p = < 0.05$), and 96 h (Chisq = 24.98; df=3; $p = < 0.001$) (Fig. 6). Until 96 h after adult whitefly release, there were 1.5-fold fewer *B. tabaci* individuals on tomatoes associated with WO3 than on the tomatoes alone. The *B. tabaci* population on tomatoes associated with WO1 was 1.5-fold lower than on tomatoes alone only 3 h after release.

However, we did not observe any difference between treatments regarding the number of eggs laid on tomato leaflets (Chisq = 0.43, $p > 0.05$). The average of number eggs collected per tray was 116 ± 43, 125 ± 58, 133 ± 41, and 135 ± 45 for tomato alone, tomato with WO1, tomato with WO2, and tomato with WO3, respectively.

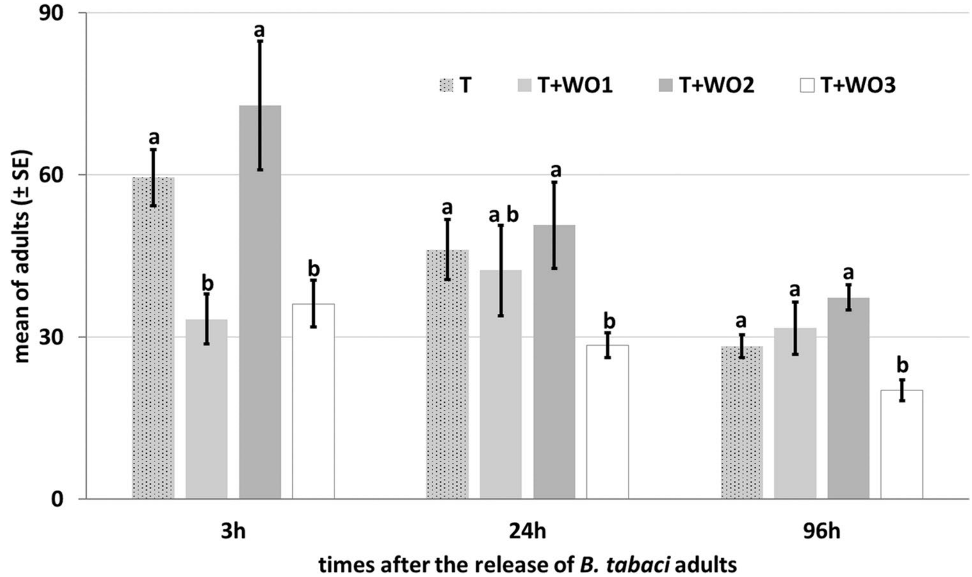

Fig. 6 Mean (± SE) of number *B. tabaci* adults on tomato according to its association with wild oregano at three times. The observations were done at three times after the release of adult whiteflies in the greenhouse. Wild oregano origins: WO1 (north), WO2 (center), WO3 (south). Means are labeled by different letters (a, b, c) significantly different from each other (Tukey post doc test, $p \leq 0.05$)

Discussion

WO EOs were repellent with either a true repellent or masking effect. The true repellent effect of WO EOs could be explained by the presence of monoterpenes, such as carvacrol, α-terpinene, and p-cymene, or sesquiterpenes, such as β-caryophyllene (Table 2). The repellency of these compounds has been reported in previous studies (Bleeker et al. 2009; Lee et al. 2019; Sadeh et al. 2017). We also showed that WO EOs sometimes had a masking effect, i.e., WO EOs at certain concentrations decreased the attractiveness of tomato. We based our study on that of Zhang et al. (2004), where they assumed that tomato plant is attractive to *B. tabaci*. Moreover, Togni et al. (2010) showed that tomato volatiles were attractant to *B. tabaci*. We suppose that the repellence effect could be due to the ratio between the two complex odors. The *B. tabaci* response would depend on the ratio between the attractants VOCs of tomato leaves and the repellent VOCs of WO EOS. This phenomenon is known for other insects. For example, flies *Drosophila melanogaster* (Meigen) (Diptera: Drosophiladae) respond to the repellent substances, benzaldehyde, 1-octen-3-ol, and geosmin according to their ratio in attractive balsamic vinegar (Verschut et al. 2019). Our results on repellency of WO EOs to *B. tabaci* are consistent with those of another study with aqueous extracts. Egg laying by *B. tabaci* was reduced on cucumber leaves (*Cucumis sativus* L.) treated with *P. amboinicus* aqueous extracts (0.3%) compared to those treated with water (Hegab et al. 2016). Our WS EO results were in agreement with those obtained by Deletre et al. (2015). However, in our study, at high concentration, WS EO no longer had the repellent effect on *B. tabaci*. This could be explained by the theory of Galizia (2014) whereby there is no linear response of the insect to the odor concentration. The olfactory receptor detects an odor at low concentration and the response increases with increasing odor concentration and then the receptor saturates. Deletre et al. (2015) did not observe any decrease in the repellent effect. In their study, they used a *B. tabaci* biotype Q population, whereas the *B. tabaci* biotype B, also called *B. argentifolii* (Bellows and Perring), is very widespread in Martinique on vegetable crops (Ryckewaert and Alauzet 2001). We suppose that the *B. tabaci* behavior would vary between these populations because of the genetic variation in the chemosensory proteins and these proteins contributed to the perception of VOCs (Liu et al. 2016). However, Deletre et al. (2015) had not done olfactometric tests with EO WS applied to tomato leaflets and Bleeker et al. (2009) did not observe differences in tomato odor perception between *B. tabaci* biotypes B and Q.

WO plant was repellent with a true repellent or masking effect and WO3 plant had a better effect than WO1 and WO2 plants. The ethanolic VOC solution of WO3, i.e., reflecting the natural emission of VOC of plants, had a true repellent effect and only WO3 plants reduced the whitefly population when intercropped with tomato. Nevertheless, we observed a reduction in the adult *B. tabaci* population when tomato was intercropped with WO but did not observe any difference in the egg laying. Our results were different with those of Hegab et al. (2016), who found that intercropping cucumbers with WO resulted in a 10% reduction of egg laying by *B. tabaci* compared to cucumbers alone. This difference in results could be due to the fact that in our study, *B. tabaci* individuals (adults and eggs) were recorded up to 4 days after release compared to the much longer period (approximately 50 days) in the other study.

Our study showed different *B. tabaci* behaviors between the three WOs likely due to different odor blends.

However, there was no difference in chemotype between the three WO origins; thus, the compound contents or ratios would play a key role in the *Bemisia* behavioral response. Despite WO daughter plants were cultivated under the same conditions to mitigate the abiotic factors, the differences between the tested WO could be due to the mother plant origins. Gouinguené and Turlings (2002) found that abiotic factors had an effect on VOCs emission. A study was conducted on *Thymus pulegioides* plants of different origins with different chemotypes and the chemotypes were found to remain stable after a change of habitat (Ložienė and Venskutonis 2005). Thereby, we assume that WO3 was better adapted to the study conditions and had a better VOC emission rate because WO3 mother plants were originally grown in Sainte-Anne where they were more subject to water stress since the annual rainfall is lower there (Table 1) and, in Vertisols, water is less available for plants during dry period (Ozier-Lafontaine and Cabidoche 1995). In our study, WO plants were grown outdoors under natural climatic conditions without irrigation.

Overall, our study showed that *P. amboinicus* was repellent against *B. tabaci* whiteflies. WO could also be used as companion plants to prevent whitefly infestation. However, although all of the plants had the same chemotype, the *B. tabaci* response depended on the plant origins. WO could also be used in pest management strategies against *B. tabaci* whiteflies through foliar application. Our study provides further insight on the potential of *P.amboinicus* as biocontrol plant for *B. tabaci* management in tomato crop fields.

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Data Availability The data that support the finding of this study are available from CIRAD Dataverse (https://doi.org/10.18167/DVN1/PGG1HT).

Declarations

Conflict of Interest The authors declare no competing interests.

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