

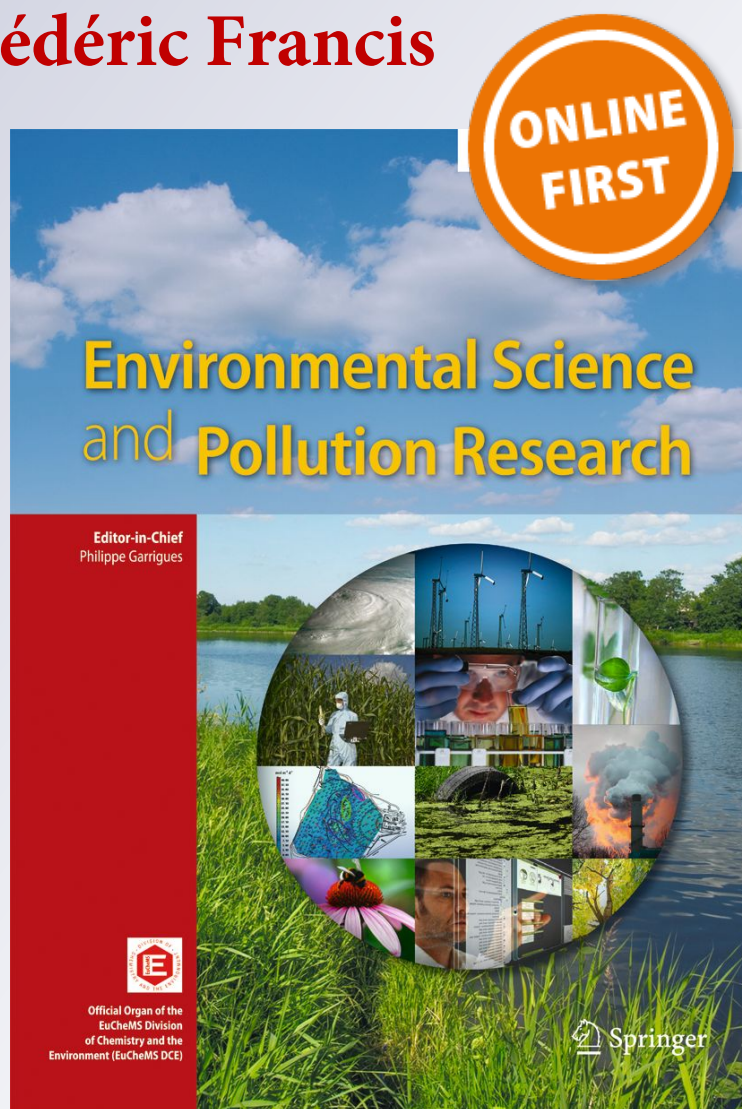
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Oviposition deterrent activity of basil plants and their essential oils against *Tuta absoluta* (Lepidoptera: Gelechiidae)

Boni Barthélémy Yarou¹ · Thomas Bawin¹ · Antoine Boullis¹ · Stéphanie Heukin² · Georges Lognay² · François Jean Verheggen¹ · Frédéric Francis¹

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Abstract The leafminer *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) is one of the most important pests of tomato, reducing crop yields by up to 100% in greenhouses and fields, in several countries globally. Because synthetic insecticides lead to resistance and have adverse effects on natural enemies and the health of producers, alternative control methods are needed. In this study, we assessed the oviposition-deterrent effect of basil plants, *Ocimum gratissimum* L. and *O. basilicum* L. (Lamiaceae), using dual-choice behavioural assays performed in flight tunnels. We found that both plants significantly reduced *T. absoluta* oviposition behaviour on a tomato plant located nearby. To evaluate the potential effect of basil volatile organic compounds, we formulated essential oils of both plant species in paraffin oil, and observed a similar oviposition-deterrent effect. Gas chromatography analyses detected 18 constituents in these essential oils which the major constituents included thymol (33.3%), p-cymene (20.4%), γ -terpinene (16.9%), myrcene (3.9%) in *O. gratissimum* and estragol (73.8%), linalool (8.6%), β -elemene (2.9%) and E- β -ocimene (2.6%) in *O. basilicum*. Twenty and 33 compounds were identified of the volatiles collected on *O. gratissimum* and *O. basilicum* plants, respectively. The main components include the

following: p-cymene (33.5%), γ -terpinene (23.6%), α -terpinene (7.2%), α -thujene (6.7%) and E- α -bergamotene (38.9%) in *O. gratissimum*, and methyl eugenol (26.1%), E- β -ocimene (17.7%), and linalool (9.4%) in *O. basilicum*. Four compounds (α -pinene, β -pinene, Myrcene, Limonene) were common in essential oils and plants. Our results suggest the valuable potential of basil and associated essential oils as a component of integrated management strategies against the tomato leafminer.

Keywords *O. basilicum* · *O. gratissimum* · Essential oil · Behaviour · Oviposition · *Tuta absoluta* · Integrated management

Introduction

Tomato, *Solanum lycopersicum* L. (Solanaceae), production is damaged by the leafminer, *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae), which is considered as one of the most important pests in both greenhouse and outdoor production (Desneux et al. 2010; Desneux et al. 2011; Campos et al. 2017). Native to South America, this Microlepidoptera has recently become an invasive pest on tomato crops in Europe (Desneux et al. 2011) and Africa (Brévault et al. 2014; Tonnang et al. 2015). *Tuta absoluta* larvae destroy all aerial parts of plants (leaves, stems, fruits, buds and flowers), resulting in severe yield losses (i.e. up to 100%) (Desneux et al. 2010; Urbaneja et al. 2013). Although tomato is the preferred host plant of *T. absoluta*, it has also been recorded, and/or develops, on other cultivated and non-cultivated plants. Its host-range includes other Solanaceae species, such as potato (*Solanum tuberosum* L.), aubergine (*Solanum melongena* L.), black nightshade (*Solanum nigrum* L.) and bitter-sweet nightshade (*Solanum dulcamara* L.). It also targets species

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from other plant families, such the Fabaceae, including the groundnut (*Arachis hypogaea* L.), cowpea (*Vigna unguiculata* L.) and bean (*Phaseolus vulgaris* L.) (Desneux et al. 2010; Bawin et al. 2015a, b).

The control of *T. absoluta* is mainly based on synthetic insecticides (da Silva Galdino et al. 2011; Valchev et al. 2013); however, these methods have limits. For instance, many active compounds, including abamectin, spinosad, indoxacarb (Siqueira et al. 2001; Campos et al. 2015); deltamethrin, methamidophos (Lietti et al. 2005); and cypermethrin, chlorpyrifos (Roditakis et al. 2013), induce the emergence of resistant pest populations. Moreover, these insecticides also negatively impact the natural enemy populations of *T. absoluta* (Arnó and Gabarra 2011; Biondi et al. 2013; Abbes et al. 2015) owing to multiple potential side effects as described by Desneux et al. (2007) in a review. The effectiveness of biological control using entomopathogenic organisms (González-Cabrera et al. 2011; Ben Khedher et al. 2015) beneficial insects (Ferracini et al. 2012; Chailleux et al. 2012; Chailleux et al. 2013; Öztemiz 2013; Salehi et al. 2016) present valuable alternative methods to synthetic pesticides. For example, the use of certain Miridae as *Macrolophus pygmaeus* Rambur or *Dicyphus maroccanus* Wagner appears to be a reliable biological alternative for the control of *T. absoluta* (Urbaneja et al. 2013; Abbas et al. 2014; Jaworski et al. 2015). Until now, prophylactic methods (Urbaneja et al. 2013) supplemented with pheromone traps (Filho et al. 2000; Vacas et al. 2011; Cocco et al. 2013) have facilitated the development of a reliable and sustainable form of management of *T. absoluta*. In addition to the methods mentioned above, plant breeding could be a promising approach for *T. absoluta* management also. Indeed, some tomato cultivars appear to be less susceptible to *T. absoluta* damage according to Sohrabi et al. (2016).

The essential oils of many plants species have been demonstrated to have beneficial effects that manipulate insect pests and reduce damage to crops (Fayalo et al. 2014; Liu et al. 2014). For instance, the biocidal effects (insecticidal, repellent) of *Ocimum* spp. (Lamiaceae) have been well studied, mainly on malaria insect vectors (Kazembe and Chauruka 2012; Belong et al. 2013; Akono Ntonga et al. 2014) and on pests of stored products (Ilboudo et al. 2010; Adeniyi et al. 2010; Koubala et al. 2013). In intercropping systems, *Ocimum* spp. are also effective in controlling additional crop pests, including moths, leaf beetles, aphids and whiteflies (Beizhou et al. 2011; Song et al. 2013). However, knowledge remains limited on how aromatic plants (especially *Ocimum* species) affect the tomato leafminer *T. absoluta*.

In this study, we evaluated the repellent and oviposition-detering effect of two *Ocimum* species, *Ocimum gratissimum* L. and *Ocimum basilicum* L., on the tomato leafminer *T. absoluta*. Both aromatic species are used as food ingredients and medicinal plants (Selvakkumar et al. 2007; Prabhu et al.

2009; Bilal et al. 2012), so they could be considered harmless to humans. Our results are expected to indicate the potential of *Ocimum* species as alternative pest biocontrol methods.

Materials and methods

Plant and insect rearing

Ocimum gratissimum (African basil) and *O. basilicum* (European basil) seeds were provided by the Vegetable Crops Program of the National Institute of Agricultural Research of Benin (INRAB), West Africa. Tomato *S. lycopersicum* cv. Moneymaker and basil plants were individually grown under greenhouse (Gembloux, Belgium, 25 ± 5 °C, 50–70% relative humidity [RH], 16:8-h light: dark photoperiod) in plastic pots ($8 \times 8 \times 9$ cm) filled with potting soil (VP113BIO, Peltracom, Belgium) and were watered every 2 days. Plants were used in experiments when they reached 4 weeks (*S. lycopersicum* and *O. basilicum*) and 6 weeks (*O. gratissimum*) after seeding (i.e. at about 20–25 cm in height).

The larvae of *T. absoluta* (third instar) were first collected in July 2011 from a commercial tomato plantation (SAS Rougeline, Saint-Andiol, France, $43^{\circ} 49' 53.1''$ N $4^{\circ} 58' 20.1''$ E). The *T. absoluta* colony was subsequently maintained on tomato plants in $45 \times 45 \times 45$ cm net cages (BugDorm, MegaView Science, Taichung, Taiwan) in a L2Q laboratory (24 ± 1 °C, 60–70% RH, and 16:8-h light: dark photoperiod).

Oviposition assays

Effect of *Ocimum* plants on *Tuta absoluta* oviposition response

Flight tunnel experiments were used to evaluate how basil plants in the vicinity of a tomato plant impacted the oviposition of *T. absoluta* adults. The flight tunnels ($230 \times 45 \times 45$ cm) were divided into three areas (Caparros Megido et al. 2014; De Backer et al. 2015, 2016): a central area for insect release and two areas at opposite sides containing the plants. Two modalities were tested: (1) a tomato plant associated with either an *O. gratissimum* or *O. basilicum* plant versus (2) a tomato plant without *Ocimum* plant (control). For each replicate, 15 unsexed *T. absoluta* adult individuals were randomly sampled from the rearing population and were released in the central area of the tunnel. After 48 h, the number of males and females in each area of the tunnel, as well as the number of eggs laid on each plant, were recorded. The experiments were conducted under the following conditions: 20 ± 1 °C, $65 \pm 5\%$ RH, and a 16:8-h light: dark photoperiod.

under cool white LED lights (77 $\mu\text{mol}/\text{sqm}/\text{s}$). These conditions were monitored using an automatic data logger (HOBO RH/TEMP 8 K; Onset Computer Corporation, Bourne, MA, USA). Six replicates were assessed for each modality (i.e. basil species association).

Effect of *Ocimum* essential oils on *Tuta absoluta* oviposition response

Essential oils (EO) from *O. gratissimum* and *O. basilicum* were purchased from local manufacturers in Benin. Two concentrations of each EO (i.e. 5 and 10 mg/ml) were formulated in paraffin oil (PO), and were tested for their oviposition deterring following the same experimental design as described in the previous section. A 1 ml cylindrical rubber septum (17 mm high \times 10 mm diameter) (VWR International, Radner, PA, USA) loaded with 100 μl solution (formulated EO or PO alone) was placed on each plant as a semiochemical dispenser. The tested modalities were: (1) a tomato plant with 100 μl of a 5 mg/ml corresponding to 0.5 mg of EO (*O. gratissimum* or *O. basilicum*) versus a tomato plant with 100 μl of PO and (2) a tomato plant with 100 μl of a 10 mg/ml corresponding to 1.0 mg of EO (*O. gratissimum* or *O. basilicum*) versus a tomato plant with 100 μl of PO. Six replicates were assessed for each treatment.

Analysis of essential oils and characterisation of plant volatiles components

Essential oil analysis of basil

Essential oil components were analysed by both gas chromatography-flame ionisation detection (GC-FID) and gas chromatography-mass spectrometry (GC-MS). GC-FID analyses were performed using an Agilent Technologies (Santa Clara, CA, USA) 6890 gas chromatograph fitted with a flame ionisation detector and capillary column HP-5 (5% Phenyl Methyl, 30 m, 0.25 mm i.d., 0.25 μm film thickness). Helium was used as carrier gas at a constant flow rate of 1.5 ml/min. The temperature program was started at 40 $^{\circ}\text{C}$ for 2 min, and then increased by 8 $^{\circ}\text{C}/\text{min}$ to 280 $^{\circ}\text{C}$, with final hold at this temperature for 5 min. Injector (splitless mode) and detector (H_2 , 35 ml/min; air, 350 ml/min) temperatures were 280 and 290 $^{\circ}\text{C}$, respectively.

GC-MS was carried out on an Agilent Technologies (Santa Clara, CA, USA) 6890 gas chromatograph coupled to an Agilent 5973 mass spectrometer. The analysis was performed under similar conditions (previous section) using a capillary column (HP-5 MS: 30 m, 0.25 mm i.d., 0.25 μm film thickness), with helium as the carrier gas. The mass spectra scanning range was set from 35 to 350 amu (EI mode at 70 eV). The components were identified by comparing the recorded

mass spectra with the Wiley 275.L spectral database using Chemstation software (Agilent Technologies, Palo Alto, CA, USA). Further identification was carried out by injecting a homologue series of n-alkanes ($\text{C}_7\text{--}\text{C}_{30}$) under identical chromatographic conditions, and calculating non-isothermal retention indices (RI). These RI were compared to those reported in the published literature (Adams 2007; Babushok et al. 2011; Pherobase 2016). Relative proportions of the components were calculated based on GC-FID peak areas using response factors of 1 for each component.

Plant volatiles analysis

To identify the volatile organic compounds (VOCs) emitted by each basil species, plants at 4 to 6 weeks after seed emergence were placed in separate 4 L glass jars to collect VOCs with solid-phase micro-extraction (SPME, 10-mm fibre with a 50/30 μm carboxen-ivinybenzene-polydimethylsiloxane coating-Supelco). Before sampling, the fibres were conditioned at 250 $^{\circ}\text{C}$ for 1 h in a GC injector. Volatiles were collected at 25 ± 1 $^{\circ}\text{C}$ for 1 h. GC-MS analyses were performed in triplicate (three SPME sampling on three different plants of each species) under the aforementioned conditions (EO analysis section). The components were identified by comparing the recorded mass spectra with the Wiley 275.L spectral database using Chemstation software (Agilent Technologies, Palo Alto, CA, USA). The relative proportion of each component was calculated by dividing the peak area of each compound by the total peak area.

Statistical analyses

Binomial proportion tests (equal distribution hypothesised) were used to compare the number of (1) females and males recorded in each area of the tunnel and (2) the number of eggs laid on basil-associated and non-associated tomato plants during the dual-choice behavioural assays. These statistical tests were performed using Minitab® v.17 software (Minitab, Coventry, UK). The significant threshold was $P < 0.05$.

Results

Effect of *Ocimum* plants on the distribution and oviposition response of *Tuta absoluta*

Both males and females were equally distributed ($P > 0.05$) on both sides of the flight tunnels in all of the tested modalities (Table 1). However, females laid significantly more eggs on non-associated tomato plants compared to tomato plants associated with *O. gratissimum* ($P < 0.001$) and *O. basilicum* ($P < 0.001$) (Fig. 1).

Table 1 Results of dual choice evaluating the distribution of *T. absoluta* associated with *Ocimum* plants (Og: *O. gratissimum*; Ob: *O. basilicum*) and essential oil (EO) and non-associated tomato plants (T). Values are the total numbers of individuals for each combination (six replicates)

Insects tested number	Responding insects (%) ^a	Choice behaviour with plants		<i>p</i> value	
96	83 (86.5)		T	T + Og	
		Males	18	14	0.59
		Females	28	23	0.58
95	73 (76.8)		T	T + Ob	
		Males	10	15	0.42
		Females	24	24	1
Choice behaviour with essentials oils					
93	64 (68.8)		T + PO	T + Og (5 mg/ml)	
		Males	8	14	0.29
		Females	22	20	0.88
88	64 (72.7)		T + PO	T + Og (10 mg/ml)	
		Males	10	9	0.80
		Females	34	18	0.03
93	73 (78.5)		T + PO	T + Ob (5 mg/ml)	
		Males	10	9	0.80
		Females	34	18	0.03
86	64 (74.4)		T + PO	T + Ob (10 mg/ml)	
		Males	10	14	0.54
		Females	17	23	0.43

^a Responding insects include living individuals present in one of the two side areas of the tunnel

Effect of *Ocimum* essential oils on the distribution and oviposition response of *Tuta absoluta*

The number of insects that responded to the EOs and the distribution of individuals are presented in Table 1. Males were equally distributed on both sides of the flight tunnels in almost all tested modalities. In contrast, *T. absoluta* female attraction differed between tomato plants associated with PO

and those associated with the EOs of either *O. gratissimum* ($P = 0.04$ with 1.0 mg) or *O. basilicum* ($P = 0.03$ with 0.5 mg). Females also laid significantly more eggs on tomato plants associated with PO compared to tomato plants associated with an *O. gratissimum* or *O. basilicum* EO dispenser, except when the dose of *O. gratissimum* was 0.5 mg (Fig. 2).

Chemical components of essential oils and plant volatiles

For each essential oil, 18 compounds were identified (Table 2). Mass spectra and RI reflected the data from the published literature (Runyoro et al. 2010; Babushok et al. 2011; Kpadonou Kpoviessi et al. 2012). Six of these compounds were common to both *Ocimum* species (α -pinene, Camphene β -pinene, Myrcene, Limonene and Borneol). Monoterpenoids were the main components, with thymol (33.3%), p-cymene (20.4%), γ -terpinene (16.9%) and myrcene (3.9%) in the EO of *O. gratissimum* EO and estragol (73.8%), linalool (8.7%), β -elemene (2.9%) and E- β -ocimene (2.6%) in the EO of *O. basilicum*. Twenty and 33 compounds were identified from plant volatile analyses for *O. gratissimum* and *O. basilicum*, respectively (Table 3). Thirteen compounds are common between the volatile blends of the two *Ocimum* species (α -thujene, α -pinene, β -pinene, Sabinene, Myrcene, α -phellandrene, δ -3-carene, α -terpinene, p-cymene, Limonene, Cis-ocimene γ -terpinene and Allo-ocimene). Monoterpenoids were, again, the main components

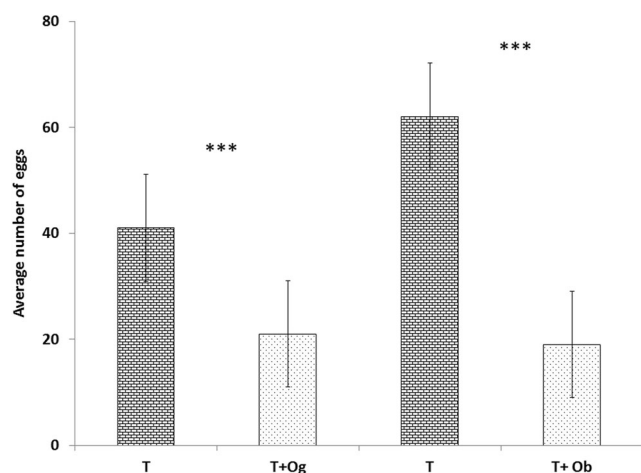


Fig. 1 Average number of eggs laid by *T. absoluta* females on a tomato plant (control) versus a tomato plant associated either with *O. gratissimum* or *O. basilicum* 2 days after releasing the insects in a dual-choice flight tunnel. Values are number (Mean \pm SE) of the total eggs laid per combination (six replicates). *** $P < 0.001$

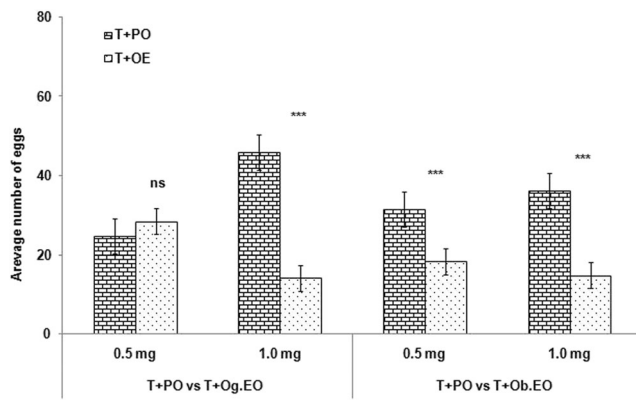


Fig. 2 Average number of eggs laid by *T. absoluta* females on a tomato plant associated with a rubber septum filled with paraffin oil versus a tomato plant with a rubber septum filled with *O. gratissimum* or *O. basilicum* essential oil 2 days after releasing the insects in a dual-choice flight tunnel. Values are number (Mean \pm SE) of the total eggs laid per combination (six replicates), *** $P < 0.001$, ns (not significant)

with p-cymene ($33.5 \pm 2.3\%$), γ -terpinene ($23.6 \pm 1.6\%$), α -terpinene (7.2 ± 0.5) and α -thujene ($6.7 \pm 0.8\%$) in *O. gratissimum* and E- α -bergamotene ($38.9 \pm 10.3\%$), methyl eugenol ($26.1 \pm 10.9\%$), E- β -ocimene ($17.7 \pm 4.0\%$) and linalool (9.4 ± 3.2) in *O. basilicum*. Four compounds (α -pinene, β -pinene, Myrcene, Limonene) were common in essential oils and plants VOCs.

Discussion

Our study demonstrated the oviposition-detering effect of *O. gratissimum* and *O. basilicum* plants and their respective essential oils against *T. absoluta*. However, no differences were found in terms of the spatial distribution of these insects in the flight tunnels. Therefore, we could not confirm that basil plants and their essential oils repel adult leafminers.

Our results about *Ocimum* oviposition-detering effect confirm those of previous studies. For instance, *O. basilicum* ethanolic extracts negatively influenced the oviposition behaviour of another leafminer *Phthorimaea operculella* Zell. (Lepidoptera: Gelechiidae) (Sharaby et al. 2009). *Ocimum* spp. essential oils were previously shown to reduce the oviposition behaviour of *Agrotis ipsilon* H. (Lepidoptera: Noctuidae) on cotton plants (Shadia et al. 2007). Moreover, *O. gratissimum*, *O. basilicum* and *O. sanctum* L. extracts or EOs were found to have a repellent and oviposition deterrent effect on the insect pests (Dryophthoridae, Curculionidae, Bostrichidae, Tenebrionidae, Bruchidae) of various stored products (Asawalalam et al. 2008; Ogendo et al. 2008; Kiradoo and Srivastava 2010). The observed reduction in eggs laid on tomato plants when associated with basil plants or essential oils demonstrates that *Ocimum* spp. had a deterred effect on the oviposition behaviour of *T. absoluta* females.

Table 2 Chemical components of the essential oils found in *O. gratissimum* (Og) and *O. basilicum* (Ob)

Compound	Og (%) ^a	Ob (%) ^a	RI ^b
α -thujene	3.6	—	926
α -pinene	1.5	0.2	934
Camphene	0.2	0.1	951
Sabinene	0.2	—	974
β -pinene	0.5	0.3	979
Myrcene	3.9	0.9	989
α -phellandrene	0.3	—	1007
δ -3-carene	0.3	—	1010
α -terpinene	1.9	—	1018
p-cymene	20.4	—	1026
Limonene	0.6	0.3	1031
E- β -ocimene	—	2.6	1047
γ -terpinene	16.9	—	1060
p-cymenene	1.5	—	1091
Estragol	—	73.9	1195
1,8-cineol	—	1.5	1034
Linalool	—	8.7	1101
Camphor	—	0.8	1150
Borneol	0.6	0.2	1169
Terpineol 4	1.9	—	1183
Methyl thymol ether	0.5	—	1231
Thymol	33.3	—	1291
β -elemene	—	2.9	1393
E-caryophyllene	—	0.1	1426
α -bergamotene	0.2	—	1435
γ -elemene	—	0.7	1437
α -guaiane	—	0.4	1440
α -humulene	—	0.2	1462
β -selinene	—	0.6	1496
γ -cadinene	—	0.9	1519

^a—'not-detected

^a Relative percentage

^b Retention index

The ability of insects to locate host plants for feeding or reproduction (eggs laying) is affected by the VOCs that it perceives (Bruce et al. 2005; Webster et al. 2010; Solé et al. 2010; Bruce and Pickett 2011). In addition to directly repelling insects, non-host odours also mask host plant volatiles (Zhang et al. 2013). Thus, in both approaches, the compound identified by our study in basil EO and VOCs might have changed the chemical environment by masking tomato VOCs and preventing *T. absoluta* females from recognising these plants. Indeed, an oviposition deterrent effect of certain compounds (such as β -caryophyllene, α -pinene, β -pinene, limonene, terpineol-4, thymol and eugenol) has been highlighted for several pests of stored food products (Regnault-Roger and Hamraoui 1995; Ferrarini et al. 2008;

Table 3 Chemical volatile organic compounds emitted by *O. gratissimum* (Og) and *O. basilicum* (Ob) plants,

Components	Og (%) ^a	Ob (%) ^a	RT ^b
α-thujene	6.7 ± 0.8	0.9 ± 0.6	10.8
α-pinene	2.5 ± 0.4	2.9 ± 1.9	11.0
Camphene	0.5 ± 0.1	–	11.5
Sabinene	0.7 ± 0.0	0.9 ± 0.3	12.2
β-pinene	1.9 ± 0.6	2.5 ± 0.6	12.3
Myrcene	3.8 ± 0.2	5.1 ± 0.9	12.7
α-phellandrene	1.0 ± 0.1	1.2 ± 0.6	13.1
δ-3-carene	0.5 ± 0.0	1.2 ± 0.4	13.3
α-terpinene	7.2 ± 0.5	1.0 ± 0.5	13.5
p-cymene	33.5 ± 2.3	4.5 ± 3.1	13.8
Limonene	3.8 ± 0.3	6.0 ± 4.4	13.9
1,8-cineole	–	2.9 ± 1.5	14.0
Cis-ocimene	0.6 ± 0.1	1.1 ± 0.3	14.1
E-β-ocimene	–	17.7 ± 4.0	14.4
γ-terpinene	23.6 ± 1.6	1.5 ± 1.3	14.8
α-terpinolene	–	3.6 ± 2.2	15.7
p-cymenene	2.6 ± 0.2	–	15.7
Linalool	–	9.4 ± 3.2	16.0
(E)-4,8-dimethyl-1,3,7-nonatriene	–	0.8 ± 0.3	16.5
Allo-ocimene	0.2 ± 0.1	2.0 ± 0.4	16.8
Neo-allo-ocimene	–	2.8 ± 0.4	17.2
Thymol methyl Ether	3.0 ± 1.3	–	19.9
Thymol	4.4 ± 3.1	–	21.4
α-cubebene	–	0.7 ± 0.3	23.1
Eugenol	–	0.5 ± 0.3	23.3
α-copaene	–	0.9 ± 0.1	23.8
β-elemene	–	1.0 ± 0.2	24.2
Methyl eugenol	–	26.1 ± 10.9	24.4
E-caryophyllene	0.8 ± 0.4	–	25.0
E-α-bergamotene	–	38.9 ± 10.3	25.3
Aromadendrene	–	0.5 ± 0.0	25.5
E-β-farnesene	–	5.0 ± 1.3	25.7
α-humulene	–	1.0 ± 0.1	25.9
Epi-bicyclosesquiphellandrene	–	0.6 ± 0.2	26.1
Ar-curcumene	–	0.6 ± 0.0	26.4
β-Selinene	1.9 ± 0.8	–	26.7
E-Methyl isoeugenol	–	2.3 ± 0.9	26.7
α-selinene	0.7 ± 0.3	–	26.9
γ-cadinene	–	1.2 ± 0.2	27.3
1S,cis-calamenene	–	2.9 ± 0.7	27.5

‘–’ not-detected

^a Relative percentage (Mean ± SD of triplicates)^b Retention time

Chaubey 2012) and also on the potato tuber moth, *P. operculella* (Sharaby et al. 2009). This finding might explain the difference in oviposition rates by *T. absoluta* females between associated and non-associated tomato plants.

Various explanations exist for the observed random distribution of adult individuals in our study. For instance, during the first moments of the trials (≤ 24 h), females made a choice to orient towards one of the two tomato plants. This choice was probably related to the perception of VOCs released by the plants, with tomato plant VOCs having well-defined proportions that characterise it and stimulate oviposition. Previous studies have confirmed that *T. absoluta* females rely on olfactory cues during host-searching and the assessment of hosts as suitable larval substrate for oviposition (Proffitt et al. 2011). A shorter observation period might have allowed us to determine the most attractive area for ovipositing females. Males are generally attracted by sex pheromones emitted by females (Ramaswamy 1988); thus, their distribution was probably influenced by the behaviour of females.

The two basil species had a similar effect on *T. absoluta* behaviour. Both species could be used to manage this pest. The fact that they had quite different chemical profiles (according to the relative proportions) could be advantageous in management schemes, as their use could be alternated to avoid insect resistance or habituation. We suggest two approaches for their use. First, EOs could be used as semiochemical diffusers in greenhouse production. However, to optimise the effectiveness of these EOs, it is important to assess the release dynamics of EOs. Second, intercropping might be a more suitable approach in developing countries, where tomato production is primarily conducted under field conditions. These two basil species are extensively used in the diet of many families, particularly in West African countries (such as Benin and Togo). In these countries, these basil species occupy an important place among vegetable crops, and are sold at local markets throughout the year. Thus, farmers might be more inclined to adopt using basil plants in association systems, providing benefits both for pest management strategies and the commercialization and consumption of basil.

To date, few studies have focused on associating tomatoes with the culturing of other plant species to manage *T. absoluta* infestations. To our knowledge, the only example in the published literature is the association of coriander herbs (*Coriandrum sativum* L.) (Apiaceae) and gallant soldier (*Galinsoga parviflora* Cav.) (Asteraceae) to reduce *T. absoluta* abundance and increase auxiliary predators, like ladybugs and spiders, when intercropping with tomato plants (Medeiros et al. 2009). Our study was the first to highlight the repellent effect of *Ocimum* species on *T. absoluta* females. The use of these species as companion plants might reduce damage to tomato plants by lowering the number of eggs laid. In conclusion, our suggested approach is relatively easy to implement, and could be combined with other methods in an integrated management strategy against *T. absoluta*. This approach could also reduce the use of synthetic insecticides, especially in the rural communities of West Africa.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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