

Role of larval host plant experience and solanaceous plant volatile emissions in *Tuta absoluta* (Lepidoptera: Gelechiidae) host finding behavior

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Abstract The tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae), is considered to be a major pest that damages tomato (*Solanum lycopersicum* L.; Solanaceae) crops in South American, European, and Mediterranean countries. This insect species is polyphagous (i.e., feeds on many types of food); hence, it could also develop on other cultivated host plants, principally solanaceous plants, such as potato (*S. tuberosum* L.; Solanaceae) and eggplant (*S. melongena* L.; Solanaceae). Therefore, we tested the hypothesis that host plant choice by adult *T. absoluta* is influenced by plant volatile organic compounds and larval host plant experience. One tomato cultivar (cv.) ‘Money-maker’ and three potato cv. ‘Charlotte’ ‘Bintje,’ and ‘Nicola’ were tested. Using a flying tunnel, we observed that females reared on tomato preferred flying toward tomato and, to a lesser extent, potato cv. ‘Charlotte.’ These preferences might be explained by the high release of terpenes by these two plants. When conducting oviposition choice assays, we found no preference between tomato and potato in the number of eggs laid by females that had been

previously reared on either host plant. This study indicates that the host finding behavior of *T. absoluta* is mediated by solanaceous volatiles, while oviposition behavior appears to depend on additional stimuli. These results provide baseline information for use in the development of new control strategies against *T. absoluta* using semiochemicals and plant breeding.

Keywords *Scrobipalpuloides absoluta* · Potato · Tomato · Volatile organic compound · Insect interaction

Introduction

Plants have evolved a range of strategies to manipulate the behavior of their insect partners, with chemical communication being used as the main strategy in plant–insect interactions (Witzany 2008; Schiestl 2010). Plants emit volatile organic compounds (VOCs) from different above (stems, leaves, flowers, and fruits) and belowground (roots) organs into the atmosphere and soil, respectively. These compounds have important roles in mediating complex

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interactions between plants and other organisms in the same ecosystem, particularly insects (Maffei 2010; Tholl et al. 2006; Dudareva et al. 2013; Unsicker et al. 2009; Dudareva et al. 2006; Gfeller et al. 2013). VOCs are involved in the attraction of insect pollinators and seed dispersers (Peñuelas and Llusà 2004; Maffei 2010). In addition, they are involved in direct and indirect plant defense against herbivores by repelling the attacking insect (Kessler and Baldwin 2001; De Moraes et al. 2001; Verheggen et al. 2013) and by attracting natural enemies that prey on or parasitize herbivorous insects (Tholl et al. 2006; Dicke et al. 2003; Kessler and Baldwin 2001). VOCs also protect plants against pathogens (Huang et al. 2012) and are involved in plant–plant communication (Beyaert and Hilker 2014; Dudareva et al. 2013). Herbivorous insects often use these volatiles as cues in long-range orientation to locate plants to feed on or sites for eggs deposition (McCormick et al. 2012; Beyaert and Hilker 2014; Harrewijn et al. 1995).

Consequently, insect management strategies based on plant VOCs involve the development of cultivars that have enhanced direct and/or indirect defense mechanisms (Schnee et al. 2006; Kang et al. 2010; Harmel et al. 2007), the use of polyculture (i.e., agricultural practices using multiple crops in the same place) (Jones and Gillett 2005; George et al. 2013; Stamps and Linit 1997), intercropping (Xie et al. 2012; Zhou et al. 2013), or the extraction of plant volatiles to develop organic pesticides or products that lure insects (Shrivastava et al. 2010; Bleeker et al. 2009; Kaplan 2012). While the chemical composition of VOCs is very complex, the majority of these compounds belong to terpenoid, fatty acid derivative, or phenolic families (Dudareva et al. 2006; Maffei 2010).

Recently, Proffit et al. (2011) showed that terpenoid VOCs are involved in the attraction and oviposition of the tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae), indicating the potential of using tomato volatiles for the biocontrol of this pest. New and effective environmentally sound control strategies (e.g., the use of natural enemies, resistant cultivars, or plant volatiles) are required to control *T. absoluta*, which is considered to be one of the major pests that damage tomato crops in South American, European, and Mediterranean countries (EPPO/OEPP 2005; Desneux et al. 2010, 2011). The tomato leafminer originates from South America, but was accidentally introduced to Spain in 2006. Subsequently, this species has spread rapidly north to the Netherlands, south to Senegal, and east to Iran (Pfeiffer et al. 2013; Desneux et al. 2010, 2011). The main host of *T. absoluta* is tomato (*Solanum lycopersicum* L.; Solanaceae); however, other cultivated host plants, principally solanaceous species, may also be attacked, including potato (*S. tuberosum* L.;

Solanaceae), eggplant (*S. melongena* L.; Solanaceae), sweet pepino (*S. muricatum* L.; Solanaceae), and tobacco (*Nicotiana tabacum* L.; Solanaceae) (Pereyra and Sánchez 2006; Galarza 1984; Garcia and Espul 1987). The ability of *T. absoluta* to develop on different potato varieties under laboratory (Pereyra and Sánchez 2006; Caparros Megido et al. 2013) and outdoor (Morrison et al. 2011; Unlu 2012) conditions is now well established. Thus, this pest could probably spread from tomato crops to nearby potato crops. Generalist species, like *T. absoluta*, are able to detect and interpret a wider range of cues produced by plant volatiles.

However, experience from previous life stages might also be used to facilitate host choice (Bernays 2001; Anderson et al. 2013). For instance, the plant species on which a mother develops may affect the composition of her eggs, which subsequently affects the growth and development of her progeny (Hopkins 1917; Mousseau and Fox 1998). In this study, we investigated the ability of adult *T. absoluta* to adjust host plant choice by using larval host plant experience and plant VOCs.

Materials and methods

Plant and insect cultures

Tomato (*Solanum lycopersicum* ‘Moneymaker,’ ‘Pyros F1’) and potato (*Solanum tuberosum* ‘Charlotte,’ ‘Nicola,’ and ‘Bintje’) plants were cultivated in a greenhouse at 25 ± 5 °C in plastic pots (20 cm diameter \times 20 cm height) that were filled with loam (VP113BIO; Peltracom, Belgium) and grown under a 16L:8D (16 h light and 8 h dark) photoperiod. The plants were watered once every 2 days.

In July 2011, 200 third instars of the tomato leafminer, *T. absoluta*, were collected from a commercial tomato plantation located in Saint-Andiol (France) and were subsequently kept under laboratory conditions at 24 ± 1 °C, 60–70 % relative humidity (RH), and under a 16L:8D photoperiod. Four separate *T. absoluta* colonies were reared and bred on tomato (‘Pyros F1’) and potato (‘Charlotte,’ ‘Nicola,’ or ‘Bintje’) crops within net cages (each cage 46.5 cm \times 46.5 cm \times 46.5 cm). Caterpillars were provided with fresh plants three times a week, until pupation. At least five generations were raised on each type of host plant before starting the experiments, to eliminate the effect of food reserves in the eggs or on the emerging larvae (Hasan and Ansari 2011). We maintained a 1:1 female/male ratio in the colonies, to avoid the parthenogenetic reproduction of the females and a consequent decrease in fitness (Caparros Megido et al. 2012).

Collection of plant volatiles

Entire plants (Tomato ‘Moneymaker’ and potato ‘Charlotte,’ ‘Nicola,’ or ‘Bintje,’ 4 weeks old with a 107 BBCH [Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie] code, number of tested plants = 4) were separately placed into 40-l glass jars that were closed with a glass lid. Before volatile collection, each glass and Teflon[®] pipe used to connect the experimental setup was washed with Extran[®] solution (MA 01; Merck, Darmstadt, Germany). In addition, each plant pot was wrapped in aluminum foil to avoid contamination from the pot and the soil. A pull air pump (Escort Elf[®] Pump, MSA, Pittsburgh, PA, USA) provided constant airflow from the bottom to the top of the jar at 1 l/min, after being charcoal-filtered with a carbon trap (Carbon Cap 75, Whatman, Maidstone, England). Volatiles were collected from each plant over a 4-h period, after a 45-min acclimation period. To collect volatile organic compounds (VOCs) released into the plant headspace, a 45-mg HayeSep Q glass trap (80/100 mesh; Hayes Separation Inc., Houston, TX, USA) was connected to the setup with a Teflon[®] pipe connecting the pump and the glass jar. A second trap was connected inline, to ensure the trap has not reached breaking point.

Before use, all of the traps were washed with 600 μ l dichloromethane and 600 μ l *n*-hexane (95 % purity; Sigma-Aldrich, St. Louis, MO, USA). After volatile collection, the traps were immediately eluted with 200 μ l *n*-hexane, after which and *n*-butyl-benzene (100 ng) was added to each sample as the internal standard. The samples were stored in closed vials wrapped with a Teflon strip at -80 °C before analysis.

Extracts were analyzed by gas chromatography coupled with mass spectrometry (GC–MS) using an Agilent Technologies (Santa Clara, CA, USA) model 6890n GC System/5973 Mass Selective Detector. Aliquots (1 μ l) were injected with a splitless injector maintained at 220 °C. The column (HP-5MS, 30 m \times 0.25 mm \times 0.25 μ m) was maintained at 35 °C for 2 min, before being heated to 100 °C at a constant rate of 5 °C/min. The column was then heated to 260 °C at a constant rate of 20 °C/min. The quantification of compounds was realized by comparing their areas with the internal standard and a response factor of 1, using Chemstation software (Agilent Technologies, Palo Alto, CA, USA).

The laboratory was maintained at 20 ± 1 °C, 65 ± 5 % RH, and a 16L:8D photoperiod under cool white light-emitting diode (LED) lights (77 μ mol/sqm/s). All conditions were monitored using an automatic datalogger (HOBO RH/TEMP 8 K; Onset Computer Corporation, Bourne, MA, USA).

Chemical identification

The components were identified by comparing the recorded mass spectra with the National Institute of Standards and Technology (NIST) and Wiley spectral databases. Further identification was carried out by calculating non-isothermal Kovats retention indices and by injecting saturated *n*-alkane standard solution (C7–C30 1,000 μ g/ml in hexane, Supelco, Belgium) under the same chromatographic conditions. Identification was confirmed by the injection of available commercial standards (termed STD in Table 1). As chromatographic conditions were identical for the analyses of both the collected compounds and the standards, compound identification was confirmed by comparing their retention data and mass spectra with those of the commercially available reference compounds.

Behavioral assays

A flying tunnel (232.5 cm \times 46.5 cm \times 46.5 cm) was used to study the preferences of *T. absoluta* toward different solanaceous plants (tomato ‘Moneymaker,’ potato ‘Bintje,’ ‘Nicola,’ and ‘Charlotte,’ 4 weeks old with a 107 BBCH code) (Fig. 1). This enclosure was divided into three parts: a central zone for insect release and two zones at opposite sites containing the plants. Sixteen newly emerged *T. absoluta* adults were placed in the neutral zone of the experimental area at a distance of 116.5 cm from each plant. After 48 h, the number of males, females, and eggs laid (under a binocular magnifier) in each zone of the experimental setup was counted. For the egg counts, only the aerial parts of the plants were checked. Each plant combination was randomly tested five times (for a total of 80 insects tested per dual choice assay), and the same combinations were tested with insects reared on tomato and potato plants. The experiments were carried out under laboratory conditions (20 ± 1 °C, 65 ± 5 % RH, and a 16L:8D photoperiod under cool white LED lights [77 μ mol/sqm/s]). These conditions were monitored using an automatic datalogger (HOBO RH/TEMP 8 K; Onset Computer Corporation, Bourne, MA, USA).

Statistical analyses

Principal component analysis (PCA) was performed on a correlation matrix for the visual comparison of the VOC profiles from the four different solanaceous plant cultivars. One-way ANOVAs were applied to compare the mean quantities of each VOC released by the four tested cultivars. Chi-square tests of independence were used to analyze the behavioral assays, by comparing the choice percentages of males and females and by comparing the number of eggs

Table 1 Amounts (ng ± SE/g of plant) of the different volatile compounds of four solanaceous plants

CAS number	IUPAC name	Compound name	Identification	Sample MS, RI	Literature MS, RI	Solanaceous plants			
						Tomato	Money maker (n = 4)	Binije (n = 4)	Potato
1	Bicyclo[3.1.1]hept-2-ene,2,6,6-trimethyl-	α -Pinene	STD, MS, RI	932.20	933a	84.78 ± 44.87a	2.19 ± 0.43a	3.97 ± 0.51a	3.23 ± 0.42a
2	Bicyclo[3.1.0]hexane, 4-methylene-1-(1-methylethyl)-	Sabinene	STD, MS, RI	969.14	973a	19.40 ± 3.87a	0.0b	0.0b	0.0b
3	Bicyclo[3.1.1]heptane, 6,6-dimethyl-2-methylene-	β -Pinene	STD, MS, RI	974.75	980a	4.72 ± 3.28a	0.0a	0.0a	0.0a
4	1,6-Octadiene, 7-methyl-3-methylene-	Myrcene	STD, MS, RI	990.84	991a	8.87 ± 2.98a	0.0b	0.0b	0.0b
5	(1R,6S)-4,7,7-Trimethylbicyclo[4,1,0]hept-4-ene	δ -2-Carene	STD, MS, RI	999.31	1,004b	127.43 ± 45.44a	0.0b	0.0b	0.0b
6	1,3-Cyclohexadiene, 2-methyl-5-(1-methylethyl)-	α -Phellandrene	STD, MS, RI	1,003.19	1,007b	27.69 ± 9.43a	0.0b	0.0b	0.0b
7	Bicyclo[4.1.0]hept-3-ene, 3,7,7-trimethyl-	δ -3-Carene	STD, MS, RI	1,008.85	1,009b	24.52 ± 16.26a	1.49 ± 0.08a	2.12 ± 0.19a	1.56 ± 0.12a
8	4-Methyl-1-propan-2-yl-7-oxabicyclo[2.2.1]heptane	1,4-Cineole	STD, MS, RI	1,014.43	1,016a	0.0a	0.0a	0.0a	0.51 ± 0.17b
9	1,3-Cyclohexadiene, 1-methyl-4-(1-methylethyl)-	α -Terpinene	STD, MS, RI	1,015.61	1,020b	4.80 ± 2.84a	0.0a	0.0a	0.0a
10	Cyclohexene, 1-methyl-4-(1-methylethyl)-	β -Phellandrene	STD, MS, RI	1,027.81	1,031a	471.73 ± 156.23a	1.82 ± 0.39b	2.12 ± 0.40b	2.32 ± 0.26b
11	1,3,3-trimethyl-2-Oxabicyclo[2,2,2]octane	1,8-Cineole	STD, MS, RI	1,030.39	1,030b	0.0a	0.0a	0.0a	0.46 ± 0.27a
12	1,3,6-Octatriene, 3,7-dimethyl-, (3Z)-	(E)- β -Ocimene	MS, RI	1,048.06	1,050a	0.0a	0.0a	0.85 ± 0.52a	0.0a
13	Butylbenzene	N-Buryl-Benzene	SI	1,055.35	/	1,000	1,000	1,000	1,000
14	Nonanal	Nonanal	STD, MS, RI	1,105.78	1,104b	13.59 ± 10.04a	1.01 ± 0.35a	0.69 ± 0.40a	1.46 ± 0.28a
15	(3E)-4,8-Dimethylnona-1,3,7-triene	4,8-Dimethyl-1,3,7-nonatriene	MS, RI	1,122.28	1,113e	0.0a	0.0a	0.0a	2.50 ± 1.45a
16	Naphthalene	Naphthalene	STD, MS, RI	1,188.20	1,179a	6.49 ± 4.89a	0.0a	0.0a	0.0a
17	1H-Cyclopent[1,3]cycloprop[1,2]benzene, 3a,3b,4,5,6,7-hexahydro-3,7-dimethyl-4-(1-methylethyl)-, (3aS,3bR,4S,7R,7aR)-	α -Cubebene	MS, RI	1,358.76	1,351a	0.0a	0.0a	0.0a	0.52 ± 0.11b
18	Tricyclo[4,4,0,0,2,7]dec-3-ene, 1,3-dimethyl-8-(1-methylethyl), (1R,2S,6S,7S,8S)-	α -Copaene	MS, RI	1,386.78	1,391a	0.0a	0.22 ± 0.15ab	0.0a	0.86 ± 0.35b
19	(1aR,4R,4aR,7aR,7bR)-1,1,4-Trimethyl-7-methylidene-2,3,4,4a,5,6,7a,7b-octahydro-1aH-cycloprop[<i>c</i>]azulene	α -Gurjunene	MS, RI	1,423.78	1,409a	0.0a	0.0a	0.0a	1.02 ± 0.41b
20	Bicyclo[7.3.0]undec-4-ene, 4,11,1-trimethyl-8-methylene, (1R,4E,9S)	β -Caryophyllene	STD, MS, RI	1,436.03	1,467b	29.28 ± 2.91ab	2.69 ± 0.40a	11.29 ± 2.51a	43.66 ± 11.13b
21	?	β -Gurjunene	STD, MS, RI	1,451.64	1,433 g	0.0a	0.37 ± 0.22a	0.0a	0.72 ± 0.29a

Table 1 continued

CAS number	IUPAC name	Compound name	Identification	Sample MS, RI	Literature MS, RI	Solanaecous plants			
						Tomato		Potato	
						Money-maker (n = 4)	Binije (n = 4)	Nicola (n = 4)	Charlotte (n = 4)
22	1,6,10-Dodecatriene, 7,11-dimethyl-3-methylene, (6E)	(E)-β-Farnesene	STD, MS, RI	1,460.84	1,458a	0.0a	0.51 ± 0.29a	4.71 ± 0.29ab	9.49 ± 2.72b
23	/	Non-identified sesquiterpene 1	/	1,465.67	/	0.0a	1.12 ± 0.38b	0.0a	0.0a
24	1,4,8-Cycloundecatriene, 2,6,6,9-tetramethyl, (1E,4E,8E)	α-Humulene	STD, MS, RI	1,471.87	1,467b	6.74 ± 0.72a	0.0b	1.16 ± 0.45b	1.99 ± 0.56b
25	1-Dodecanol	Dodecanol	STD, MS, RI	1,476.73	1,468c	0.0a	0.0a	0.0a	3.18 ± 0.52b
26	1,6-Cyclododecadiene, 1-methyl-5-methylene-8-(1-methylethyl), (1E,6E,8S)-	Germaerene-D	MS, RI	1,498.65	1,499a	0.0a	3.29 ± 0.43a	5.52 ± 0.87a	33.95 ± 8.84b
27	24703-35-3 (4E,8E)-4,8,11,11-Tetramethylbicyclo[8.1.0]undeca-4,8-diene	Bicyclogermaerene	MS, RI	1,514.97	1,500g	0.0a	0.0a	1.852 ± 0.162a	5.645 ± 1.428b
28	20307-83-9 3-[(2S)-6-Methylhept-5-en-2-yl]-6-methylidene-cyclohexene	β-Sesquiphellandrene	MS, RI	1,535.27	1,543b	0.0a	0.0a	1.143 ± 0.466ab	1.947 ± 0.722b
29	62235-06-7 4,8,12-trimethyl-1,3,7,11-tridecatetraene	(E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene	MS, RI	1,583.38	1,569d	33.849 ± 19.65a	0.0a	0.0a	1.267 ± 0.862a
30	5986-49-2 1,1,4,7-Tetramethyl-2,3,4,5,6,7,7a,7b-octahydro-1aH-cyclopropa[h]azulen-4a-ol	Palustral	MS, RI	1,593.47	1,569f	0.0a	0.0a	0.0a	0.715 ± 0.278b
31	?	Germaerene-D-4ol	MS, RI	1,597.96	1,574a	0.0a	2.197 ± 0.332a	8.329 ± 2.051ab	18.718 ± 5.318b
32	1139-30-6 5-Oxatricyclo[8.2.0.0,4,6]dodecane, 4,12,12-trimethyl-9-methylene, (1R,4R,6R,10S)-	Caryophyllene oxide	STD, MS, RI	1,610.00	1,583f	0.0a	0.0a	0.0a	0.97 ± 0.431b
33	/	Non-identified sesquiterpene 2	/	1,631.65	/	0.0a	0.0a	0.0a	3.595 ± 0.894b
Total						863.89 ± 278.45a	16.94 ± 1.81b	43.74 ± 5.61b	140.29 ± 34.99b

a = Pherobase (2013), b = Flavornet (2013), c = Jennings and Shibamoto (1980), d = Turlings et al. (1991), e = Azuma et al. (1997), f = Gbolade et al. (2009), and g = Adams (2007)

MS = comparison of mass spectra with those of Nist08 and Wiley 275 libraries, RI = comparison of retention indices with those reported in the literature, STD = comparison of retention time and mass spectra of available standards

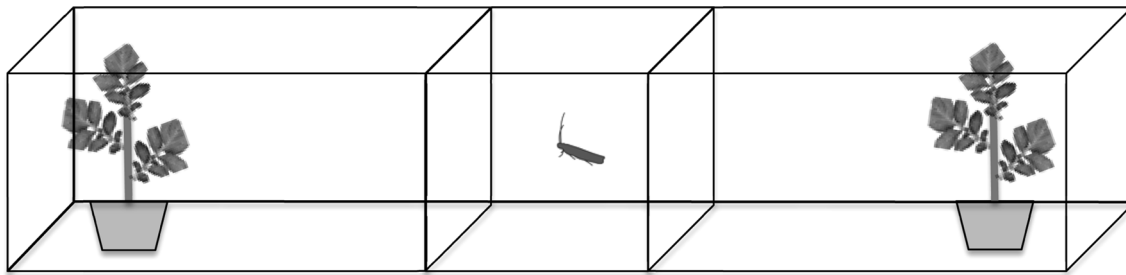


Fig. 1 Flying tunnel (232.5 cm × 46.5 cm × 46.5 cm) used to study the preferences of *T. absoluta* toward different solanaceous plants (tomato cv. Moneymaker, potato cv. 'Bintje,' 'Nicola,' and

'Charlotte'). This enclosure is divided into three parts, a central zone for the insect release and two zones containing plants, and situated on the two opposite sites

laid by females on each studied cultivar (the results of the five behavioral assay replicates were pooled together). All tests were performed using Minitab® v.16 software (<http://www.minitab.com/fr-FR/default.aspx>).

Results

Analysis of plant volatiles

Gas chromatographic analyses performed on plant volatile extracts were used to draft the VOC profile of each plant cultivar (Fig. 2). A total of 33 compounds were found in the headspace of all of the tested plants, of which 31 were identified (Table 1). Compounds commonly associated with the earth's atmosphere (e.g., toluene and benzene), as well as compounds associated with the analytical system (e.g., siloxanes or phthalates), were excluded from the list (Jansen et al. 2009). In addition, volatile chemicals identified only in one of the four replicates were not included. The terpenoids (principally mono- and sesquiterpenes) were the most abundant of these compounds. Tomato released larger amounts of β -phellandrene (compound number 10 in Table 1, $F_{3,15} = 9.04$, $P = 0.002$) and α -humulene (24, $F_{3,15} = 33.51$, $P < 0.001$) compared to the three potato cultivars, and was the only tested plant to release sabinene (2), myrcene (4), δ -2-carene (5), α -phellandrene (6), and α -terpinene (9) (Table 1, Fig. 2). In comparison, potato cv. 'Charlotte' released larger amounts of β -caryophyllene (20, $F_{3,15} = 9.69$, $P = 0.002$), (*E*)- β -farnesene (22, $F_{3,15} = 10.29$, $P < 0.001$), germacrene-D (26, $F_{3,15} = 13.72$, $P < 0.001$), bicyclgermacrene (27, $F_{3,15} = 12.42$, $P < 0.001$), β -sesquiphellandrene (28, $F_{3,15} = 4.89$, $P = 0.019$), and germacrene-D-4-ol (31, $F_{3,15} = 8.62$, $P = 0.003$) compared to all other plants, and released eight compounds that were absent from the other three plants, including 1,4-cineole (8), α -cubebene (17), α -copaene (18), α -gurjunene (19), dodecanol (25), palustrol (30), caryophyllene oxide (32), and an unidentified sesquiterpene (33) (Table 1; Fig. 2). 'Nicola' and 'Bintje' produced a similar

volatile blend, except for an unidentified sesquiterpene (23), which was only found in 'Bintje.' The potato cv. 'Nicola' did not release any additional compounds compared to the other cultivars. The most abundant compound released in the headspace of tomato and potato cv. 'Bintje' was β -phellandrene (54.6 % of the total amount of emitted compounds by this cultivar) and germacrene-D (19.4 %), respectively. β -caryophyllene was the most abundant volatile in potato cv. 'Nicola' (25.8 %) and 'Charlotte' (31.1 %). Finally, the total amount of VOCs released by tomato was significantly higher compared to the three potato cultivars ($F_{3,15} = 8.20$, $P = 0.003$).

PCA was used to visually compare the volatile emissions of the tested plants (Fig. 3). This analysis confirmed the observed differences in the volatile profiles of the tested plants. Tomato and potato cv. 'Charlotte' had clearly different VOC emissions compared to the other two plants. In comparison, potato cv. 'Nicola' and 'Bintje' released a similar volatile blend, as shown on the first (47.8 %) and the second axis (28.2 %) of the PCA.

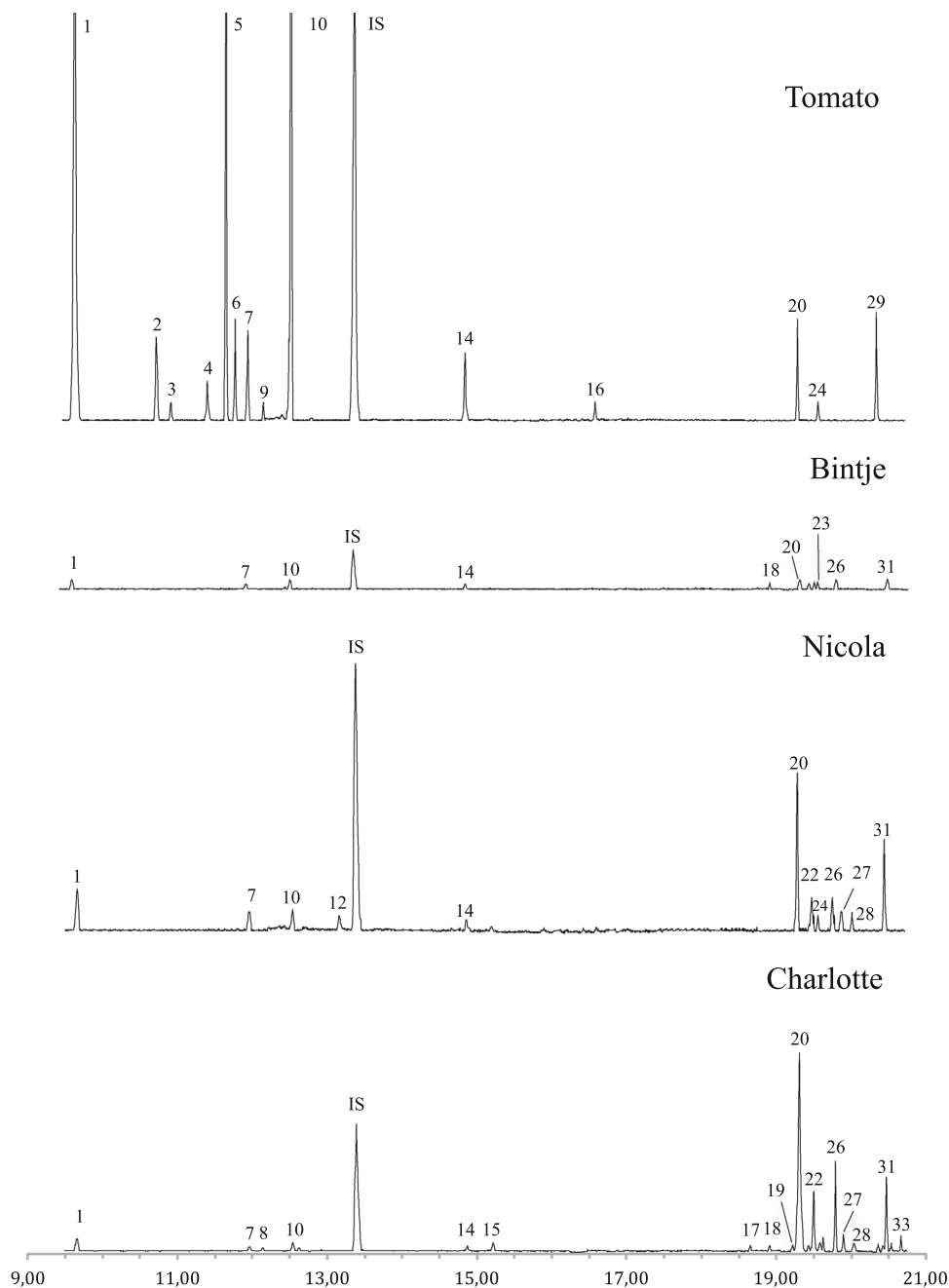
Behavioral assays

None of the four solanaceous plants attracted adult (males and females) *T. absoluta* that had been reared on potato, nor males that had been reared on tomato (Table 2). Females reared on tomato made a choice in all tested combinations of host plant and were preferentially attracted by tomato plants, followed by potato cv. 'Charlotte,' 'Nicola,' and finally 'Bintje.' Regardless of the plant variety that the insects were reared on, females laid more eggs on the most attractive plant between the two proposed plants, even if, in some cases, this attraction was not statistically significant (Table 2).

Discussion

Tuta absoluta is considered to be a polyphagous species (Desneux et al. 2010). For example, it is known to develop

Fig. 2 Chromatograms of VOCs emitted by four solanaceous plants (the number on peaks refers to the compound number given in Table 1, *IS* internal standard)



and reproduce on different tomato and potato cultivars under laboratory conditions, in greenhouses, and on agricultural land (Caparros Megido et al. 2013; Proffit et al. 2011; Unlu 2012; Gharekhani and Salek-Ebrahimi 2013; Ecole et al. 2001; Oliveira et al. 2009; Giustolin et al. 2001). During the plant-host location phase, *T. absoluta* females detect small differences in the odor blend of tomato cultivars and adapt their oviposition behavior according to plant volatile cues (Proffit et al. 2011). In this study, the attraction of *T. absoluta* to four different solanaceous plant cultivars was evaluated in a bioassay. This

study shows that tomato-reared *T. absoluta* females were more attracted to tomato plants compared to potato plants (in the order of ‘Charlotte,’ ‘Nicola,’ and ‘Bintje’). This result was expected because tomato is considered to be the ideal host for *T. absoluta* development (Pereyra and Sánchez 2006; Miranda et al. 1998). In addition, it is known that moth females preferentially oviposit on plant species on which they previously developed (Moreau et al. 2008; Olsson et al. 2006).

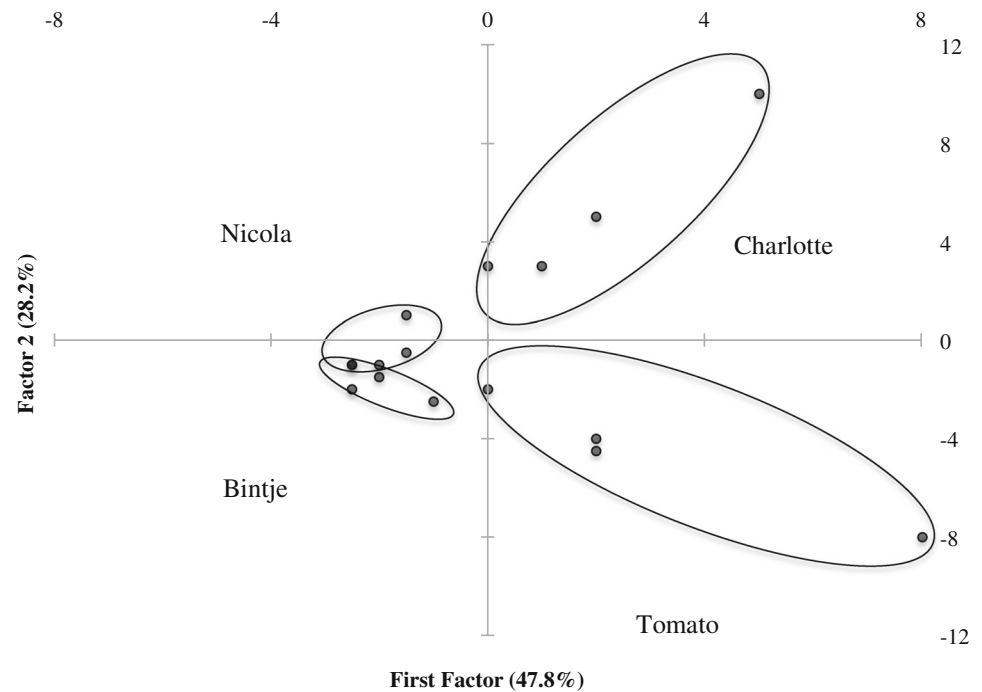
Host plant choice is important for Lepidoptera fitness (Thompson 1988; Thompson and Pellmyr 1991). The neonate

Table 2 Results of behavioral assays ($n = 5$ for each double choice; *Pyr* Pyros F1, *Mon* Moneymaker, *Cha* Charlotte, *Bi* Bimtje, *Nic* Nicola)

Rearing source	Plant A	Plant B	Sex	Number of tested insects	Responding insects (%)	Preferred plant	Number of insects on the preferred plant	Statistical analyses	<i>P</i>	Eggs laid (%)		Statistical analyses	<i>P</i>
										Plant A	Plant B		
<i>Pyr</i>	Cha	Bi	M	41	25 (61)	Cha	18 (72 %)	$\chi^2 = 2.31$	0.128	37 (74)	13 (26)	$\chi^2 = 11.52$	0.001
			F	39	35 (90)	Cha	22 (63 %)	$\chi^2 = 6.00$	0.014				
<i>Nic</i>	Cha	Bi	M	38	22 (58)	/	11 (50 %)	$\chi^2 = 0.00$	1.000	32 (74)	11 (26)	$\chi^2 = 10.26$	0.001
			F	42	36 (86)	Cha	23 (64 %)	$\chi^2 = 2.31$	0.128				
<i>Pyr</i>	Bi	Nic	M	34	19 (56)	Nic	12 (63 %)	$\chi^2 = 0.88$	0.346	28 (34)	55 (66)	$\chi^2 = 8.78$	0.003
			F	46	43 (93)	Nic	28 (65 %)	$\chi^2 = 3.93$	0.047				
<i>Cha</i>	Bi	Nic	M	32	20 (63)	Nic	12 (60 %)	$\chi^2 = 0.22$	0.637	25 (35)	47 (65)	$\chi^2 = 6.72$	0.010
			F	48	45 (94)	Nic	27 (60 %)	$\chi^2 = 1.80$	0.180				
<i>Pyr</i>	Nic	Cha	M	34	21 (62)	Cha	13 (62 %)	$\chi^2 = 1.19$	0.275	14 (22)	49 (78)	$\chi^2 = 19.44$	0.001
			F	46	43 (94)	Cha	31 (73 %)	$\chi^2 = 9.09$	0.003				
<i>Bi</i>	Nic	Cha	M	40	29 (73)	Cha	18 (62 %)	$\chi^2 = 1.69$	0.194	28 (35)	51 (65)	$\chi^2 = 6.69$	0.010
			F	40	36 (90)	Cha	23 (64 %)	$\chi^2 = 2.78$	0.096				
<i>Pyr</i>	Mon	Nic	M	39	30 (77)	Mon	17 (57 %)	$\chi^2 = 0.53$	0.465	49 (69)	22 (31)	$\chi^2 = 10.27$	0.001
			F	41	36 (88)	Mon	26 (72 %)	$\chi^2 = 7.81$	0.005				
<i>Bi</i>	Mon	Nic	M	36	27 (75)	Mon	15 (56 %)	$\chi^2 = 0.33$	0.564	55 (66)	29 (34)	$\chi^2 = 8.05$	0.005
			F	44	39 (89)	Mon	25 (64 %)	$\chi^2 = 3.60$	0.058				
<i>Pyr</i>	Mon	Cha	M	31	22 (71)	Mon	14 (64 %)	$\chi^2 = 1.80$	0.180	59 (70)	25 (30)	$\chi^2 = 13.76$	0.001
			F	49	47 (96)	Mon	33 (70 %)	$\chi^2 = 7.37$	0.007				
<i>Nic</i>	Mon	Cha	M	33	17 (52)	/	8 (47 %)	$\chi^2 = 0.00$	1.000	52 (65)	28 (35)	$\chi^2 = 7.20$	0.009
			F	47	44 (94)	Mon	30 (68 %)	$\chi^2 = 2.47$	0.116				
<i>Pyr</i>	Mon	Bi	M	35	26 (74)	Mon	16 (62 %)	$\chi^2 = 1.81$	0.178	55 (70)	24 (30)	$\chi^2 = 12.16$	0.001
			F	45	42 (93)	Mon	28 (67 %)	$\chi^2 = 5.23$	0.022				
<i>Cha</i>	Mon	Bi	M	31	23 (74)	Mon	13 (57 %)	$\chi^2 = 0.43$	0.513	58 (64)	33 (36)	$\chi^2 = 6.87$	0.009
			F	49	45 (92)	Mon	29 (64 %)	$\chi^2 = 3.60$	0.058				

Bold values indicate significant results

Fig. 3 Spatial distribution of the volatile blend released by tomato ('Moneymaker') and potato (cv. ' Bintje,' 'Charlotte,' 'Nicola') ($n = 4$)



larvae of many species are unable to move to an alternative food source and are dependent on their mother's choices (Feeny et al. 1983; Portier 1949). Classically, both males and females are attracted to the odor blends released by plants, which signal food sources, mating sites, or larval host plants (Trona et al. 2010). However, in this study, *T. absoluta* reared on potato plants did not exhibit any preferences in dual choices with potato and tomato plants. These insects might be simultaneously attracted by the plant on which they were exposed during their entire development (potato) and by the volatile blend of the plant that their ancestors were reared on (tomato) as the appropriate food source.

The larval host plant did not influence host acceptance (adult oviposition) in the current study, because both tomato- and potato-reared females laid similar amounts of eggs on both plants offered during the experiments. It has been long hypothesized that female oviposition preferences are directly influenced by larval experience (Hopkins 1917). However, the results of the current study indicate that while *T. absoluta* larval experience might influence adult female host searching behavior, it only has a weak influence on oviposition behavior. This finding might be explained by the fact that, during host searching, females only rely on olfactory cues, whereas, during oviposition, females are exposed to a variety of cues, including plant volatiles, contact chemicals, and visual signals, which help determine the characteristics of the plant (e.g., secondary metabolite production, phenology, tissue hardness, and defense mechanisms) to confirm their choice (Olsson et al. 2006; Awmack and Leather 2002; Costa et al. 2009).

Tuta absoluta males that were reared on either tomato or potato plants did not show any preferences toward any of the four tested cultivars. In non-feeding species, like *T. absoluta*, males primarily use olfaction to detect conspecific female sex pheromones, whereas females primarily rely on olfactory cues to locate and identify appropriate larval substrate for oviposition (Ramaswamy 1988; Olsson et al. 2006). Moreover, while plant odors might influence the male response to female sex pheromones (Trona et al. 2010), males rarely exhibit adaptive behavior in response to host plant volatiles, as shown for females (Anderson et al. 2013).

This study confirmed that the four tested cultivars produced plant volatiles with different compositions and quantities of compounds. These differences might explain the host searching behavior response exhibited by females during the behavioral assays. Tomato was clearly the most preferred plant by *T. absoluta* females, followed by potato cv. 'Charlotte,' 'Nicolas,' and 'Bintje.' Tomato and potato cv. 'Charlotte' appeared to be the most attractive plants in the behavioral assays. The tomato cultivar primarily released a blend of monoterpenes, with large amounts of α -pinene, sabinene, myrcene, δ -2-carene, α -phellandrene, δ -3-carene, β -phellandrene, and one sesquiterpene (β -caryophyllene). In comparison, potato cv. 'Charlotte' primarily released a blend of sesquiterpenes, with large amounts of β -caryophyllene, (*E*)- β -farnesene, germacrene-D, and germacrene-D-4-ol. These findings partially support previous studies on tomato ('Moneymaker') (Reisenman et al. 2013; Jansen et al. 2009; Fraser et al. 2003) and potato

(‘Surprise,’ ‘Princess,’ ‘Agria,’ and ‘Désirée’) (Bolter et al. 1997; Laothawornkitkul et al. 2010; Karlsson et al. 2009; Gosset et al. 2009) cultivars. Tomato also released a small amount of α -terpinene and α -humulene, while ‘Charlotte’ released different minor compounds, such as 1,4-cineole, α -cubebene, α -copaene, α -gurjunene, dodecanol, bicyclogermacrene, β -sesquiphellandrene, palustrol, and caryophyllene oxide.

Previous studies have already characterized the VOCs released by the tomato cv. ‘Moneymaker,’ in addition to recording the presence of some alcohol and aldehyde compounds, which were not observed in the volatile collection of the current study (Fraser et al. 2003; Jansen et al. 2009; Reisenman et al. 2013). Differences in the volatile profile might be explained by the use of cut plants, rather than entire plants (as in the current study), in the previous studies. It is known that mechanical damage in plants could induce an immediate release of VOCs that are chemically different to those induced by undamaged plants, including alcohols, aldehydes, and acetates (Turlings et al. 1998). In addition, the phenological stage of the plant might also influence the composition of VOCs being released and explain the different volatile blends that were observed (Beyaert and Hilker 2014; Najar-Rodriguez et al. 2010). Published studies on the VOCs released by ‘Charlotte,’ ‘Nicola,’ and ‘Bintje’ are not available. However, in addition to the classical set of terpenes found in potatoes, Karlsson et al. (2009) also identified different alcohols, aldehydes, and benzenoids. These differences in the volatile profile might, again, be explained by the use of cut plants, rather than entire plants. For instance, Bolter et al. (1997) studied entire potato plants (‘Surprise’) and obtained very similar volatile profiles to those presented in our study. These results imply that entire plants provide more representative profiles of the natural volatile blend released by plants compared to cut plants.

Minimal differences were obtained for the volatile profile of the tested plants in the current study compared to previous studies. Twenty-two of the identified compounds were highly released by two most attractive plants (i.e., tomato and potato cv. ‘Charlotte’). These compounds could be considered as major candidates in the research of VOCs that induce the long-range attraction of *T. absoluta* females. It has already been confirmed that some of the highly released compounds (i.e., sabinene, myrcene, β -caryophyllene, (*E*)- β -farnesene, germacrene-D, and germacrene-D-4-ol), as well as some of the minor compounds (i.e., α -cubebene and α -copaene), elicit antennal responses in *Tecia solanivora*, which is a potato pest belonging to the Gelechiidae family (Karlsson et al. 2009).

To confirm the effect of one specific chemical (or blend of the 22 mentioned compounds) on the attraction of *T. absoluta*, further electrophysiological and behavioral

assays are required. Such assays should focus on both the major and minor compounds, because minor constituents in a blend might also play an important role in host plant location (Najar-Rodriguez et al. 2010; Tasin et al. 2011). In conclusion, this study confirmed that *T. absoluta* females use volatile cues to select and oviposit on certain plants. Thus, while this species is likely to use tomato plants preferentially, pest control schemes should be developed to prevent this species transferring to certain potato cultivars.

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