



Influence of non-host aromatic plants on the survival and olfactory behavior of the African citrus psyllid, *Trioza erytreae*

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Abstract

Trioza erytreae Del Guercio, 1918, commonly known as the African citrus psyllid, is one of the main vectors of Huanglongbing (citrus greening), the most destructive citrus disease worldwide. Currently, there is no effective treatment for HLB; therefore, management efforts primarily focus on controlling the insect vectors. This often involves the use of insecticides, which raises concerns about environmental impact and the development of insecticide resistance. This study evaluates the potential of five aromatic non-host plants commonly found in the Mediterranean basin, which overlap with regions of citrus production (*Cistus ladanifer*, *Rosmarinus officinalis*, *Foeniculum vulgare*, *Lavandula stoechas*, and *Thymus mastichina*) to influence the survival and olfactory behavior of *T. erytreae*. Although the psyllids were able to survive for several days on these non-host plants, survival was significantly lower compared to the citrus host (*Citrus limon*), with *C. ladanifer* having the most detrimental effect. Olfactory assays revealed that, in females, *C. limon*, *C. ladanifer*, and *L. stoechas* elicited significantly higher probabilities of attraction compared with *R. officinalis* and *T. mastichina*. In males, *C. limon* elicited a significantly higher probability of attraction than *R. officinalis*, *T. mastichina*, and *L. stoechas*. A total of 123 volatile organic compounds (VOCs) were identified across all plant species, of which 48 were found to be important for the olfactory response of *T. erytreae*. Among these, 19 VOCs were positively correlated with psyllid attraction, while 15 showed negative correlations, indicating a potential repellent or disruptive effect. These results suggest that specific VOCs emitted by aromatic non-host plants can modulate host-seeking behavior in *T. erytreae*, highlighting their potential application in the development of semiochemical-based, environmentally sustainable strategies for citrus pest management.

Keywords *Cistus ladanifer* · Huanglongbing · Olfactometer · Plant–insect interactions · Volatile organic compounds

Introduction

Trioza erytreae Del Guercio, 1918 (Hemiptera: Triozidae), commonly known as the African citrus psyllid, is a vector of *Candidatus Liberibacter africanus* (CLaf), the bacterium associated with citrus greening disease, or Huanglongbing (HLB), in Africa (Bové 2006). More recently, *T. erytreae* has also been confirmed as a competent vector of *Candidatus Liberibacter asiaticus* (CLas), the bacterial species most associated with HLB pandemics in Asia and the Americas (Reynaud et al. 2022). HLB currently has no cure and causes progressive decline in citrus trees, reducing yield and fruit quality, eventually leading to tree death (Cifuentes-Arenas et al. 2022; Bassanezi et al. 2009; Ghosh et al. 2022). As a result, HLB is regarded as the most destructive disease of commercial citrus crops globally (Bové 2006).

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In the absence of a cure, current management strategies primarily focus on controlling the insect vectors to limit the spread of the disease (Alqu  zar et al. 2022). In the case of *T. erytreae*, the management strategy relies on a combination of regulatory (quarantine) measures, cultural practices, sanitation efforts, including the removal of infected plants, and the application of broad-spectrum insecticides (Alqu  zar et al. 2022). In some regions, biological control using the parasitoid *Tamarixia dryi* has been implemented with success (P  rez-Rodr  guez et al. 2024). However, while these tactics have contributed to limiting the spread and population growth of *T. erytreae*, they present several challenges. The reliance on chemical insecticides raises concerns about environmental impact, non-target effects, and the potential for insecticide resistance (Yi et al. 2020; Wan et al. 2025; Zhou et al. 2025). Additionally, classical biological control may not always provide sufficient suppression under high pest pressure or across heterogeneous agricultural landscapes (Messing and Brodeur 2018). There is a growing need for sustainable, ecologically sound alternatives that can complement existing practices and reduce reliance on chemical inputs.

One promising area of pest management research focuses on the manipulation of insect behavior through semiochemicals, particularly volatile organic compounds (VOCs) emitted by plants. Aromatic plant species are well-known sources of VOCs that can repel or confuse phytophagous insects by interfering with their ability to detect and locate host plants (Yan et al. 2020; Makhoul et al. 2024; Bedini et al. 2024). Such chemical interference may occur through direct repellence, masking of host-derived olfactory cues, or disruption of psyllid orientation and landing behaviors (Yan et al. 2020; Benhadi-Mar  n et al. 2021; Barman et al. 2016). This approach has already shown potential for controlling the Asian citrus psyllid *Diaphorina citri*, the primary HLB vector in the Americas and Asia. In those systems, the intercropping of citrus with aromatic non-host plants such as guava (*Psidium guajava*) or chili pepper (*Capsicum annuum*) has resulted in reduced psyllid abundance and lower incidence of HLB (Barman et al. 2016; Ichinose et al. 2012; Gottwald et al. 2014; Zaka et al. 2010; Onagbola et al. 2011). Additionally, a study conducted by Yan et al. (2020) reported that *D. citri* also exhibited high repellence to the volatiles of five aromatic plant species.

Despite increasing attention to these chemical ecology-based tactics in *D. citri* management, much less is known about how *T. erytreae* responds to non-host plant volatiles. Nevertheless, previous studies have shown that *T. erytreae* exhibits specific olfactory responses to host plant-emitted volatile compounds. For example, Benhadi-Mar  n et al. (2021) reported that female *T. erytreae* exhibited a higher frequency of visits and shorter latency in response to lemon volatiles compared to bitter orange. Similarly,

Antwi-Agyakwa et al. (2019) demonstrated that both sexes of *T. erytreae* were attracted to a synthetic blend of lemon terpenes, limonene, sabinene, and β -ocimene, while avoiding a six-component blend that excluded these key compounds. Building on this evidence of olfactory sensitivity to host-related volatiles, it is plausible that *T. erytreae* may also respond behaviorally to volatiles emitted by aromatic non-host plants. Given the shared ecological niche and overlapping host plant preferences between *T. erytreae* and *D. citri* (Magalh  es et al. 2025), exploring the psyllid's response to non-host plant volatiles could reveal repellent or disruptive cues. Identifying such volatiles could pave the way for the development of behavior-based management tactics, including push-pull systems (Cook et al. 2007) or intercropping schemes (Gottwald et al. 2014), aimed at interfering with host location and reducing infestation pressure in citrus orchards.

Moreover, non-host plants may play an additional ecological role by serving as temporary refuges or by influencing psyllid survival in the absence of suitable hosts (Pec et al. 2024; Zhang et al. 2019; George et al. 2022). During dispersal events, especially when host plants are scarce, *T. erytreae* may land on and temporarily use non-host plants as alternative substrates. This behavior gains particular importance given that females are capable of flying up to 394.58 m at an average speed of 6.45 m/min in a single flight, as demonstrated by Rodrigues et al. (2025) using a flight mill device. Such mobility increases the likelihood of contact with non-host plants across heterogeneous landscapes. Therefore, understanding the behavioral and physiological responses of *T. erytreae* to non-host aromatic plants is essential for evaluating their potential role within integrated pest management strategies.

In this study, we evaluated the potential of five non-host aromatic plants (*Cistus ladanifer*, *Rosmarinus officinalis*, *Foeniculum vulgare*, *Lavandula stoechas*, and *Thymus mastichina*) commonly found in citrus-growing regions of the Mediterranean basin to influence the survival and olfactory behavior of *T. erytreae*. The main objectives were to assess whether these plants could (1) influence the survival of *T. erytreae*, (2) interfere with adult psyllids' attraction, and (3) disrupt their host-finding behavior.

Materials and methods

Insect rearing

Trioza erytreae individuals were reared on 1–2-year-old *Citrus limon* (cv. Lunario) plants in an insectary maintained at 23 ± 5   C, $70 \pm 10\%$ relative humidity (RH), and a photoperiod of 14 h:10 h (light: dark).

Selection and rearing of the plants

Five species of aromatic plants belonging to three different families were selected: *C. ladanifer* (Cistaceae), *R. officinalis* (Lamiaceae), *F. vulgare* (Apiaceae), *L. stoechas* (Lamiaceae), and *T. mastichina* (Lamiaceae). The selection of plants was based on their distribution and abundance in the Mediterranean region, as they are among the most abundant aromatic plants in the areas surrounding citrus orchards. The plants were approximately 2 years old at the time of the experiment and were in the vegetative growth stage. They were grown in plastic pots (20 cm in height, 11 cm in diameter) and placed in rearing chambers set at 25 °C, with 50% relative humidity, and a 16:8 h (L:D) photoperiod. To ensure optimal growth, the plants were regularly fertilized with a slow-release, complex, granular blue fertilizer with an NPK (nitrogen, phosphorus, potassium) ratio of 12–8–16. *Citrus limon* plants were also grown under the same conditions.

Survival trials

Newly emerged adults of *T. erytrae* (less than 1 h old) were sexed and individually confined in conical polypropylene cages. Each cage was 15.5 cm high, with a maximum diameter of 11.5 cm at the base and a minimum of 7.5 cm at the top. Open at both ends, they were positioned on 13 cm diameter Petri dishes, with tulle covering the top for ventilation (Fig. 1a).

Inside, two small containers filled with water and sealed with parafilm were placed. One container held a 10 cm branch of the tested plant species, while the other featured a lid with a hole containing a submerged sponge strip (Vileda) to provide a continuous water supply for the insects. In the control group, only water was provided. The cages were maintained in a climate chamber set to 23 ± 1 °C, 60–70% RH, and a 16:8 h (L:D). The plant branches and water were replaced every 1–2 days, and survival was monitored daily until the insects' death. A total of 15 replicates were conducted for each plant species and sex.

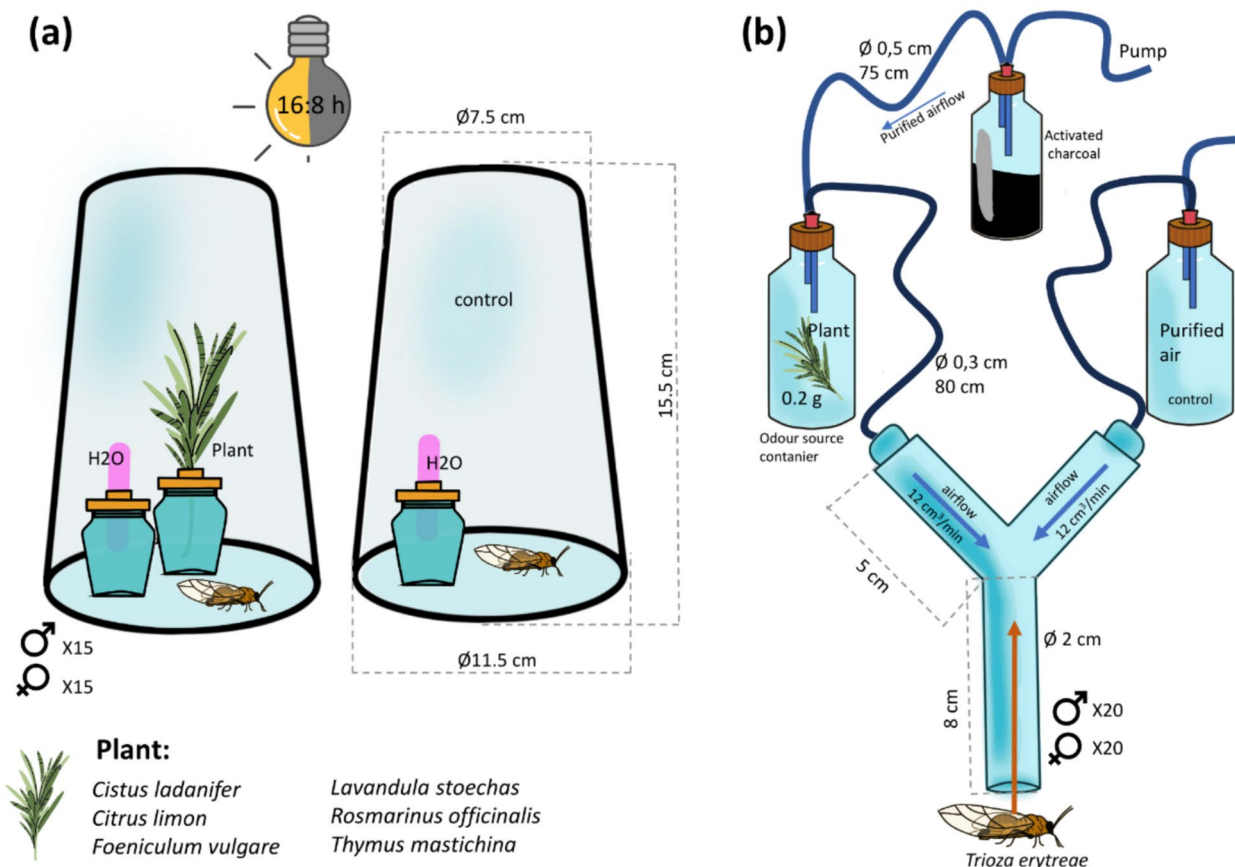


Fig. 1 Schematic drawing of the experimental setup for the **a** survival trials and for the **b** olfactory response (not drawn to scale)

Olfactory response

A glass Y-tube olfactometer (Fig. 1b) was used to evaluate the behavioral responses of 5-day-old *T. erytrae* to different plant species. The apparatus consisted of a central stem that split into two arms, each connected to a 50 mL vial. These vials were connected to 250 mL gas washing bottles containing activated charcoal (AppliChem, Panreac ITW ©) dissolved in 100 mL of distilled water, which served to purify and humidify the airflow. Vacuum pumps (type N86KN.18; $P_{\max} = 2.4$ bar; KNF Neuberger Inc.) coupled to single flow tube rotameters (Model P, 082–02-N, AALBORG®) maintained the airflow at a constant rate of 120 mL/min. To ensure uniform horizontal illumination during the tests, white LED lamps were used (dimensions: 30×1.4 cm; specifications: 6000 K, 6 W, 600 lumens, and 125 $\mu\text{m}/\text{Mol}^{-1}$). All tests were conducted in a climate-controlled room at 23 ± 1 °C with 60–70% RH, free from external light interference. To minimize potential directional biases, the Y-tube was rotated after each test.

Before the assay, the insects were individually placed in 2 mL Eppendorf tubes in the absence of food or odours for 2 h to enhance their responsiveness to olfactory stimuli. For the olfactory response test, one of the vials was loaded with 0.2 g of freshly collected plant branches. Branches of similar size and age were selected to ensure consistency across tests. The cut ends of the branches were sealed using odourless wax to prevent the release of undesired volatiles from the damaged tissues. The other vial, serving as the control, contained only purified air. New plant branches were used each time a new insect was tested, ensuring consistent olfactory cues. Between tests, the olfactometer and vials were cleaned.

Each insect was individually placed at the entrance of the olfactometer and given up to 5 min to choose between the two arms. Insects that failed to make a choice within this time were excluded from further analysis. Males and females of *T. erytrae* were tested separately to account for any sex-specific responses. For each plant species and sex, a minimum of 40 individuals demonstrating olfactory responses were ensured. A total of 256 males and 264 females were tested in the experiment, with 8% of insects excluded due to failure to make a choice within the allotted time (Supplementary Table 1).

Volatile profile

The volatile profiles of the plants under study were determined using solid-phase microextraction (SPME) coupled with gas chromatography–mass spectrometry (GC–MS). Branches weighing approximately 0.2 g were freshly cut from each plant, ensuring uniformity in size and age across samples. To prevent the release of undesired volatiles from the cut ends, each branch's cut area was isolated by dipping

it three times in heated odorless candle wax, allowing the branch to cool for 5 min.

Each prepared branch was then placed in a 100 mL glass vial submerged in a water bath maintained at 25 °C. An internal standard of 5 μL benzaldehyde (Sigma-Aldrich, St. Louis, MO, USA) at a concentration of 0.127 mg/mL was added to each vial. The headspace within the vial was stabilized for 5 min before SPME sampling. Under these conditions, an SPME fiber (divinylbenzene/carboxen/polydimethylsiloxane [DVB/CAR/PDMS], 50/30 μm ; Supelco, Bellefonte, PA, USA), previously conditioned according to the manufacturer's instructions to prevent carry-over effects, was inserted into the vial headspace for 30 min to adsorb the volatile compounds. This 30-min exposure time was established after a series of preliminary tests indicated that exposure times exceeding 30 min led to sensor saturation.

The fiber was then immediately transferred to the injection port of the chromatograph, maintained at 220 °C, and desorbed in splitless mode for 1 min. To ensure complete cleaning and prevent carry-over between samples, the fiber remained in the injection port for an additional 10 min between analyses. Additionally, blanks were analyzed between samples by exposing the fiber to empty vials and candle wax to check for any residual compounds and confirm the absence of contamination.

This procedure was carried out in quintuplicate for each of the six plant species under study. The analyses were performed using a Shimadzu GC-2010 Plus gas chromatograph equipped with a Shimadzu GC/MS-QP 2010 SE mass spectrometer and a TRB-5MS column (30 m×0.25 mm×0.25 μm). The injector operated in splitless mode (1 min) at 220 °C. Helium (Alphagaz from Air Liquide, Portugal) was used as the carrier gas at a linear velocity of 30 cm/s and a flow rate of 24.4 mL/min.

The oven temperature program was as follows: an initial temperature of 40 °C held for 1 min, increased at 2 °C/min to 180 °C to allow for the separation of low-boiling compounds, then increased at 10 °C/min to 220 °C, and held at 220 °C for 5 min to elute higher-boiling compounds. The mass spectrometer operated with an ionization source temperature of 250 °C, electron ionization energy of 70 eV, and a scan range of 35–500 m/z.

Identification of volatile compounds was achieved by comparing the obtained mass spectra with those in the NIST 11 (National Institute of Standards and Technology, Gaithersburg, MD, USA) database, using a similarity percentage threshold of $\geq 85\%$ as the identification criterion. Kováts retention indices were calculated using a series of n-alkane standards (C8–C20) run under the same chromatographic conditions and compared with literature values from the NIST 69, PubChem, and ChemSpider databases to confirm compound identities. The compound areas were determined by integrating the total ion chromatogram (TIC).

Semi-quantification of volatile compounds was achieved by converting the relative area of each peak into a mass equivalent to that of the internal standard using the following equation:

$$Y(\mu\text{g of internal standard equivalents/g of plant}) = \frac{A_y \times m_{\text{IS}}}{A_{\text{IS}}}$$

where Y represents the concentration of the volatile compound, A_y is the peak area of the volatile compound, m_{IS} is the mass of the internal standard in the sample, and A_{IS} is the peak area of the internal standard.

Data analysis

All statistical analyses were conducted using RStudio version 2023.06.0 Build 421 (R Core Team 2023). To assess the survival of *T. erytreae* across different plant treatments, Kaplan–Meier survival curves were generated using the *ggsurvplot* function from the *survminer* package (Kassambara and Kosinski 2017). Differences in survival distributions among treatments were analyzed using the log-rank test via the *survdif* function from the *survival* package (Therneau 2023). Additionally, pairwise comparisons between treatments were performed using the *pairwise_survdif* function from the same package.

The olfactory response of *T. erytreae* to different plant species was analyzed using a generalized linear model (GLM) with a binomial error distribution and a logit link function. The response variable was the insect's choice in the Y-tube olfactometer, coded as 1 for the plant odor arm and 0 for the control air arm. Plant species, sex, and their interaction (plant $\times$ sex) were included as fixed effects in the model. The model was fitted using the *glm()* function in the *stats* package (R Core Team 2021). Model significance was assessed using an analysis of deviance with likelihood ratio tests, comparing nested models using ANOVA from the *stats* package (R Core Team 2021).

To compare plant species within each sex, post-hoc pairwise comparisons were conducted using estimated marginal means (EMMs), as implemented in the *emmeans* package (Lenth 2022). Pairwise contrasts among plant species were calculated separately for females and males, with Sidak correction applied to adjust p -values for multiple comparisons. To assess the adequacy of the model, residual diagnostics were performed using the *DHARMA* package (Hartig 2020). Simulation-based residuals were generated, and overdispersion, outliers, and residual uniformity were checked. No significant issues were identified, indicating that the model provided an adequate fit for the data.

To identify the most influential VOCs affecting the olfactory response of *T. erytreae*, a Random Forest (RF) analysis was conducted using the *randomForest* package

(Breiman et al. 2024). The importance of each VOC was determined based on the Gini Importance Measure (GIM), where higher values indicate a greater impact on insect response. VOCs with a GIM greater than two were selected for further analysis. Additionally, a Principal Component Analysis (PCA) was conducted using the function *pca* from the 'FactoMineR' package (Lê et al. 2008). The correlation biplot of the first two PCs was drawn using the *fviz_pca_biplot* function from the 'factoextra' package (Kassambara and Mundt 2020). The biplot was generated with the *fviz_pca_biplot* function from the same package.

To explore the relationship between the most influential VOCs and the olfactory response of *T. erytreae*, a Pearson correlation analysis was performed using the *cor.test* function from base R. The Pearson correlation coefficient (r) was calculated for each compound, along with its corresponding p -value to assess statistical significance. The results were visualized using a bar plot generated with the *ggplot2* package (Wickham 2016).

Results

Survival test

Kaplan–Meier plots and the log-rank test were used to analyze the survival of *T. erytreae* females and males on *C. limon* (positive control), water (negative control), and five different aromatic plants (Fig. 2). Survival rates varied significantly across treatments (females: $\chi^2 = 154$, $df = 6$, $p < 0.001$; males: $\chi^2 = 132$, $df = 6$, $p < 0.001$).

In both sexes, the lowest survival rates were observed in the control (water) treatment, with insects living significantly shorter lives compared to all other plants (all $p < 0.001$). In the absence of any plant material, females survived for a maximum of three days, while males survived only two. In contrast, *C. limon* provided the most favourable conditions for survival, with both males (53 days) and females (68 days) living significantly longer than those exposed to water or any of the aromatic plants (all $p < 0.001$).

For females, *C. ladanifer* showed the lowest survival probability among the aromatic plants, with a statistically significant difference compared to the other plants. However, no significant differences were found in female survival among *R. officinalis*, *F. vulgare*, *L. stoechas*, and *T. mas-tichina* (all $p > 0.05$) (Fig. 2a). Regarding males, survival probabilities did not differ significantly between *T. mas-tichina* and *F. vulgare* ($p = 0.79$). However, both of these plants supported significantly higher survival rates compared to *R. officinalis*, *L. stoechas*, and *C. ladanifer* (all $p < 0.05$) (Fig. 2b).

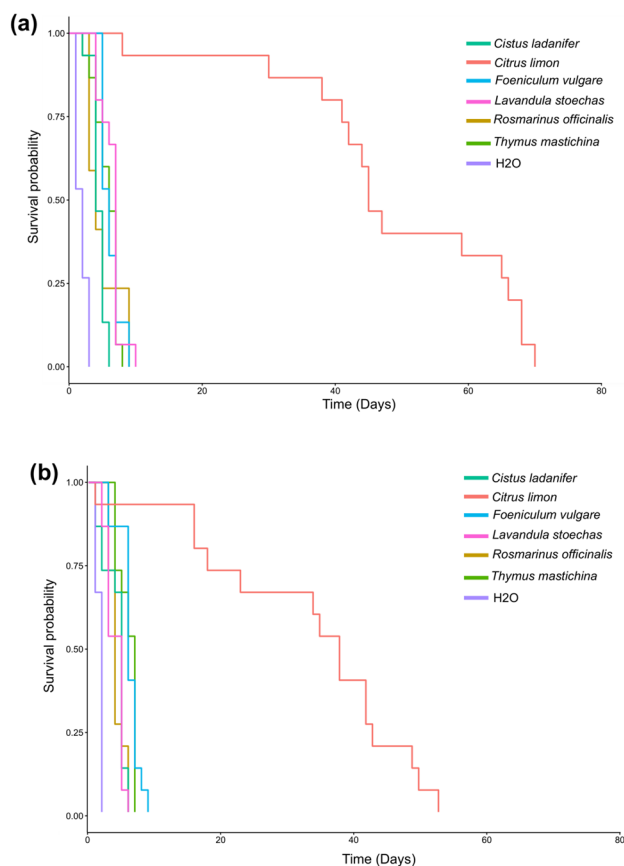


Fig. 2 Kaplan–Meier plots showing the survival probabilities of *Trioxa erythrae* **a** females and **b** males on aromatic plants (*Cistus ladanifer*, *Foeniculum vulgare*, *Lavandula stoechas*, *Rosmarinus officinalis*, and *Thymus mastichina*), with *Citrus limon* as the positive control and only water (H₂O) as the negative control

Olfactory response

The olfactory response of *T. erythrae* was significantly influenced by plant species ($\chi^2 = 62.31$, $df = 5$, $p < 0.001$). In contrast, sex alone did not have a significant main effect on the probability of choosing the plant odor arm ($\chi^2 = 1.68$, $df = 1$, $p = 0.19$). However, the interaction between plant species and sex was significant ($\chi^2 = 14.20$, $df = 5$, $p = 0.01$), indicating that the effect of plant species on olfactory response differed between females and males.

In females, *C. limon*, *C. ladanifer*, and *L. stoechas* elicited significantly higher probabilities of attraction compared with *R. officinalis* and *T. mastichina* (all $p \leq 0.03$). *Foeniculum vulgare* did not differ significantly from *R. officinalis* ($p = 0.06$) but had a significantly higher attraction probability than *T. mastichina* ($p = 0.0007$). However, *F. vulgare* did not differ significantly from *C. ladanifer* ($p = 1$), *L. stoechas* ($p = 1$), or *C. limon* ($p = 0.56$) (Fig. 3).

In males, *C. limon* elicited a significantly higher probability of attraction than *R. officinalis* ($p = 0.0007$), *T. mastichina* ($p = 0.04$), and *L. stoechas* ($p = 0.02$). No significant differences were detected among *R. officinalis*, *T. mastichina*, *C. ladanifer*, and *F. vulgare* ($p \geq 0.50$), indicating generally similar attraction levels among these plant species in males (Fig. 3).

Volatile profile

A total of 123 VOCs were identified from the six plant species under study (Supplementary Table 2). Recognizing that not all compounds have the same importance on the olfactory response of *T. erythrae*, we conducted a Random Forest analysis to identify the VOCs as most important. Only the compounds with a GIM greater than 2 were considered (Supplementary Fig. 1), resulting in a subset of 48 compounds for further investigation (Table 1).

Among the plant species analyzed, *C. limon* exhibited the highest number of influential VOCs (21), followed by *C. ladanifer* (19), *L. stoechas* (18), *R. officinalis* (15), *T. mastichina* (14), and *F. vulgare* (9) (Table 1).

Cistus ladanifer showed a high concentration of 2,2,6-trimethyl-cyclohexanone, camphene, 2,6-dimethyl-cyclohexanol, and D-limonene. *Citrus limon* exhibited elevated concentrations of (Z)-3-hexenyl acetate and D-limonene. *Foeniculum vulgare* was characterized by a prominent concentration of fenchone, followed by p-cymene. Meanwhile, *L. stoechas* presented predominant amounts of camphor, fenchone, and eucalyptol, and *R. officinalis* displayed higher levels of p-cymene, borneol, and camphor. Finally, *T. mastichina* recorded significant amounts of eucalyptol and borneol (Table 1).

Principal Component Analysis (PCA) further underscored the distinct volatile profiles among the plant species, with the first two principal components accounting for 58.8% of the total variance (Fig. 4). The biplot revealed clearly defined clusters for certain species while others showed considerable overlap, suggesting similarities in their volatile compositions. *Cistus ladanifer* and *C. limon* formed a highly distinct group in the upper left and right quadrants, respectively. *Lavandula stoechas* and *F. vulgare* were positioned in proximity, reflecting similar volatile profiles, while *T. mastichina* and *R. officinalis* overlapped, indicating very similar VOC compositions.

Relationship between volatile profiles and olfactory response

Among the 48 influential VOCs selected, 19 VOCs showed a significantly positive correlation with the olfactory response of *T. erythrae*, while 15 VOCs exhibited a

significantly negative correlation (Fig. 5). The remaining 15 VOCs did not show any significant correlation with the olfactory response of *T. erythrae*. Although these correlations were generally low, they were statistically significant (all $p < 0.001$), likely due to a consistent but weak association across a sufficiently large sample size. This suggests that, although the effects are subtle, they are unlikely to be due to random chance. Borneol and Terpinen-4-ol showed the highest negative correlations, while D-Limonene and (Z)-3-Hexen-1-ol showed the highest positive correlations.

Discussion

Understanding the interactions between *T. erythrae* and its host and non-host plants is crucial for determining how non-host plants can affect the attraction, survival, and

colonization of citrus groves by this psyllid. Our study assessed the survival and preference of both male and female *T. erythrae* to five aromatic plants, non-host species, commonly found in abundance in areas adjacent to citrus groves in the Mediterranean region.

The results demonstrate that the survival of *T. erythrae* is significantly influenced by the plant species. The Kaplan–Meier analysis showed that individuals exhibited higher survival on *C. limon*, confirming it as one of the preferred hosts, as supported by the literature (Aidoo et al. 2019; Benhadi-Marín et al. 2021; Moran 1968; Urbaneja-Bernat et al. 2020). In contrast, the aromatic plants under study significantly reduced the survival of this insect over time. Exposure only to H₂O (negative control) resulted in the lowest survival, reinforcing that the observed effects in the tested aromatic plants are not solely due to the absence of food. These findings suggest that aromatic plants may not provide the necessary resources for the long-term survival

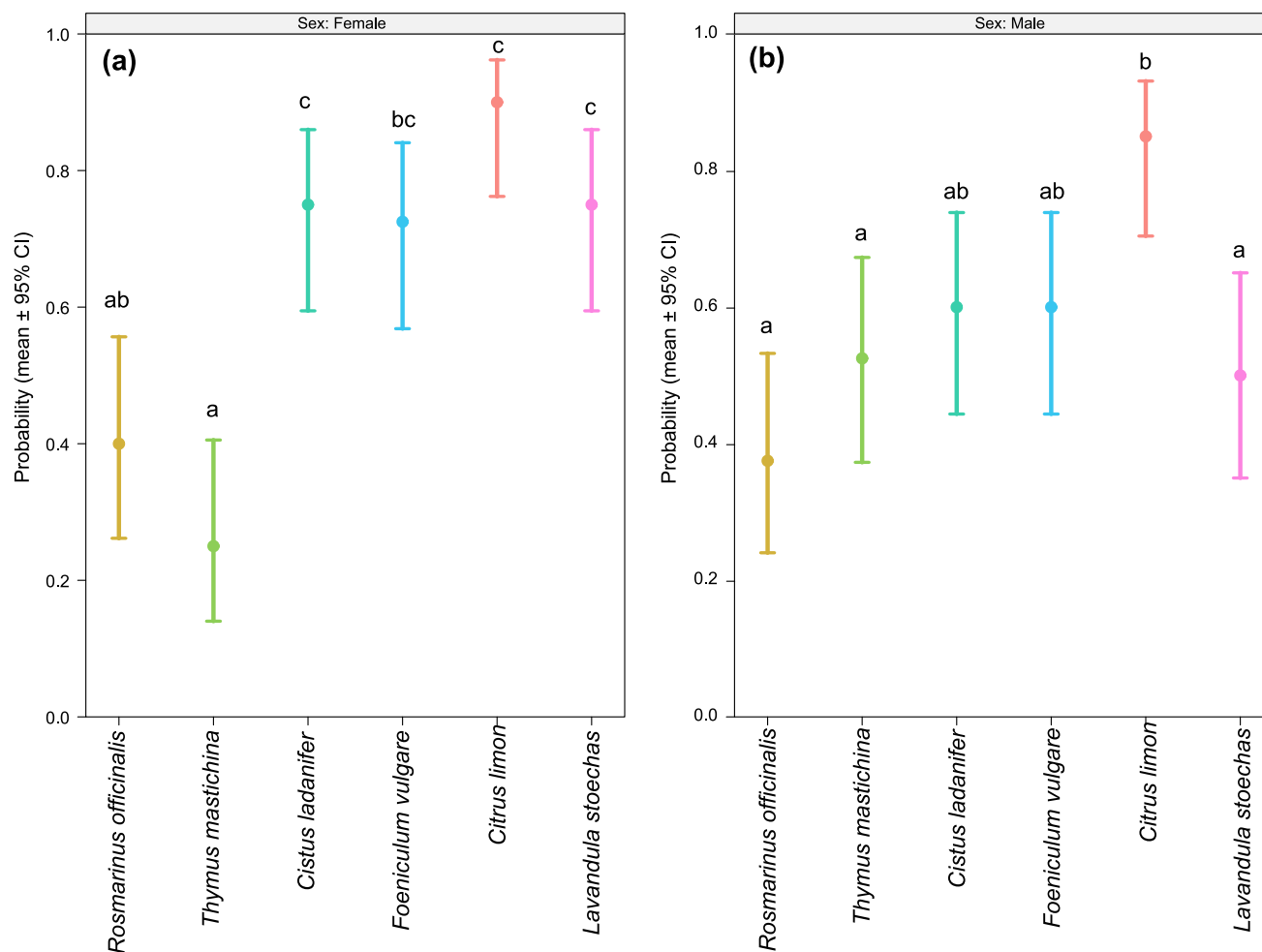


Fig. 3 Predicted mean attraction probabilities with 95% confidence intervals (vertical bars) for **a** females and **b** males to *Cistus ladanifer*, *Citrus limon*, *Foeniculum vulgare*, *Lavandula stoechas*, *Rosmarinus*

officinalis, and *Thymus mastichina*. Plant species with different letters are significantly different from each other ($p < 0.05$)

Table 1 Semi-quantitative emission levels (mean $\pm$ SE μ g IS equivalents/g) of the most influential VOCs affecting the olfactory response of *Trioza erytreae* (GIM ≥ 2) emitted by *Cistus ladanifer*, *Citrus limon*, *Foeniculum vulgare*, *Rosmarinus officinalis*, and *Thymus mastichina*

Family	Compound	<i>Cistus ladanifer</i> Mean $\pm$ SE μ g IS equivalents/g	<i>Citrus limon</i> Mean $\pm$ SE μ g IS equivalents/g	<i>Foeniculum vulgare</i> Mean $\pm$ SE μ g IS equivalents/g	<i>Lavandula stoechas</i> Mean $\pm$ SE μ g IS equivalents/g	<i>Rosmarinus officinalis</i> Mean $\pm$ SE μ g IS equivalents/g	<i>Thymus masti- china</i> Mean $\pm$ SE μ g IS equivalents/g
Alcohol	(Z)-3-Hexen-1-ol	4.00 $\pm$ 2.99	2.07 $\pm$ 0.70	nd	nd	nd	nd
	2,6-Dimethylcyclohexanol	13.85 $\pm$ 2.16	nd	nd	nd	nd	nd
Aldehyde	Citronellal	nd	0.05 $\pm$ 0.04	nd	nd	nd	nd
	Decanal	nd	0.10 $\pm$ 0.03	nd	nd	nd	nd
	Heptanal	nd	0.05 $\pm$ 0.01	nd	nd	nd	nd
	trans-Citral	nd	1.85 $\pm$ 1.26	nd	nd	nd	nd
	Dodecanal	nd	0.02 $\pm$ 0.01	nd	nd	nd	nd
Ester	(Z)-3-Hexenyl Acetate	nd	13.60 $\pm$ 9.59	nd	nd	nd	nd
	Methyl Benzoate	nd	2.19 $\pm$ 0.85	nd	nd	nd	nd
	Methyl Hexanoate	nd	0.11 $\pm$ 0.07	nd	nd	nd	nd
	Methyl Octanoate	nd	0.04 $\pm$ 0.02	nd	nd	nd	nd
	Methyl Salicylate	nd	0.10 $\pm$ 0.07	nd	nd	nd	nd
	2-(2-Butoxyethoxy)ethanol	nd	0.10 $\pm$ 0.02	nd	nd	nd	nd
Hydrocarbon	β -Bisabolene	nd	0.15 $\pm$ 0.08	nd	nd	nd	nd
	Dodecane	nd	0.05 $\pm$ 0.03	nd	nd	nd	nd
	Tetradecane	nd	nd	0.09 $\pm$ 0.04	nd	nd	nd
Ketone	6-Methyl-2-heptanone	0.82 $\pm$ 0.09	nd	nd	nd	nd	nd
	2,2,6-Trimethylcyclohexanone	25.87 $\pm$ 5.14	nd	nd	nd	nd	nd
	3-Methyl-2-cyclohexen-1-one	3.41 $\pm$ 0.51	nd	nd	nd	nd	nd
	Acetophenone	0.22 $\pm$ 0.08	nd	nd	nd	nd	nd
	α -Isophorone	nd	nd	nd	0.43 $\pm$ 0.30	nd	nd
Lactone	2(5H)-Furanone, 5,5-Dimethyl-	nd	nd	nd	0.59 $\pm$ 0.75	nd	nd
Terpene	Fenchol	nd	nd	0.08 $\pm$ 0.03	0.50 $\pm$ 0.34	nd	nd
	α -Terpineol	0.08 $\pm$ 0.02	0.09 $\pm$ 0.07	nd	0.14 $\pm$ 0.06	1.49 $\pm$ 0.74	2.00 $\pm$ 1.24
	2-Hydroxycineole	nd	nd	nd	0.12 $\pm$ 0.06	nd	nd
	Camphene	16.28 $\pm$ 2.20	nd	0.36 $\pm$ 0.07	2.17 $\pm$ 0.94	3.74 $\pm$ 1.01	0.59 $\pm$ 0.08
	Camphene Hydrate	0.18 $\pm$ 0.02	nd	nd	0.16 $\pm$ 0.14	nd	nd
	Camphor	0.66 $\pm$ 0.08	nd	0.36 $\pm$ 0.17	64.96 $\pm$ 49.24	13.60 $\pm$ 5.51	1.69 $\pm$ 0.59
	Caryophyllene	nd		nd	0.02 $\pm$ 0.02	0.08 $\pm$ 0.04	0.13 $\pm$ 0.07
	Caryophyllene Oxide	nd	0.63 $\pm$ 0.41	nd			
	cis-Rose Oxide	0.39 $\pm$ 0.30	nd	nd	nd	nd	nd
	cis-Sabinene Hydrate	0.08 $\pm$ 0.05	0.04 $\pm$ 0.02	0.12 $\pm$ 0.06	0.17 $\pm$ 0.12	2.88 $\pm$ 1.06	0.56 $\pm$ 0.22
	D-Limonene	7.22 $\pm$ 3.29	10.28 $\pm$ 7.35	nd	nd	nd	nd
	Eucalyptol	nd	nd	nd	37.15 $\pm$ 20.55	8.09 $\pm$ 2.73	105.04 $\pm$ 16.41

Table 1 (continued)

Family	Compound	<i>Cistus ladanifer</i> Mean $\pm$ SE μ g IS equivalents/g	<i>Citrus limon</i> Mean $\pm$ SE μ g IS equivalents/g	<i>Foeniculum vulgare</i> Mean $\pm$ SE μ g IS equivalents/g	<i>Lavandula stoechas</i> Mean $\pm$ SE μ g IS equivalents/g	<i>Rosmarinus officinalis</i> Mean $\pm$ SE μ g IS equivalents/g	<i>Thymus masti- china</i> Mean $\pm$ SE μ g IS equivalents/g
	Fenchone	nd	nd	81.46 $\pm$ 46.24	53.71 $\pm$ 37.07	nd	nd
	Germacrene D	nd	0.08 $\pm$ 0.06	nd	nd	nd	nd
	Myrtenol	nd	nd	nd	nd	0.21 $\pm$ 0.08	2.64 $\pm$ 0.58
	<i>p</i> -Cymene	1.98 $\pm$ 0.53	nd	9.72 $\pm$ 1.85	1.98 $\pm$ 1.50	40.38 $\pm$ 14.68	5.64 $\pm$ 1.30
	Terpinen-4-ol	0.17 $\pm$ 0.06	nd	0.04 $\pm$ 0.01	0.09 $\pm$ 0.05	4.43 $\pm$ 1.78	1.00 $\pm$ 0.29
	trans-Carveol	nd	nd	nd	nd	nd	0.14 $\pm$ 0.08
	trans-Pinocarveol	nd	nd	nd	0.08 $\pm$ 0.06	0.19 $\pm$ 0.07	1.28 $\pm$ 0.26
	trans-Sabinene Hydrate	0.20 $\pm$ 0.06	nd	nd	0.22 $\pm$ 0.23	1.18 $\pm$ 0.48	0.54 $\pm$ 0.17
	Tricyclene	4.10 $\pm$ 0.48	nd	nd	0.43 $\pm$ 0.19	0.20 $\pm$ 0.06	nd
	Verbenol	nd	0.04 $\pm$ 0.02	nd	nd	nd	nd
	α -Bergamotene	nd	0.34 $\pm$ 0.25	nd	nd	nd	nd
	β -Caryophyllene	nd	nd	nd	nd	1.14 $\pm$ 0.43	nd
	Borneol	3.61 $\pm$ 0.48	nd	0.12 $\pm$ 0.04	5.54 $\pm$ 4.17	13.84 $\pm$ 5.78	25.75 $\pm$ 5.96
	cis-Linalool Oxide	0.53 $\pm$ 0.29	nd	nd	nd	0.21 $\pm$ 0.15	1.62 $\pm$ 0.68

of *T. erytraeae*. However, this insect may temporarily colonize such species to seek refuge and water. Similar results have been reported for the other HLB vector, *D. citri*, which also exhibited an initial survival on different non-host plants. However, its survival probability declined over time, with a significantly higher survival rate on the preferred host (Martini et al. 2013; George et al. 2022; Pec et al. 2024; Zhan et al. 2019).

In olfactory assays, males and females of *T. erytraeae* were attracted to *C. limon*, aligning with the survival data. This finding underscores the importance of volatiles emitted by *C. limon* in host selection, suggesting that these chemical cues play a crucial role in attracting *T. erytraeae*. Interestingly, females also have higher attraction probabilities to *C. ladanifer*, *L. stoechas*, and *F. vulgare*. Volatile profile analysis demonstrated that both *C. limon* and *C. ladanifer* emit D-limonene and (Z)-3-Hexen-1-ol, compounds positively correlated with the olfactory response of *T. erytraeae* (see Fig. 5). This suggests that these volatiles may serve as key attractants for this psyllid species. Previous studies on *D. citri* have reported that this psyllid is consistently attracted to D-limonene (Li et al. 2024; Liu et al. 2021; Mann et al. 2012). For example, Liu et al. (2021) tested 12 highly expressed volatiles from host plants and found that D-limonene elicited strong electrophysiological (EAG) responses and significantly attracted *D. citri* adults. However, the field effectiveness of D-limonene remains

inconclusive; Pullock et al. (2024) reported that sticky traps supplemented with D-limonene did not significantly improve *T. erytraeae* captures, suggesting that isomeric variations or other environmental factors may influence its attractiveness. Regarding (Z)-3-Hexen-1-ol, a green leaf volatile known to attract *D. citri* (Zheng et al. 2023), to our knowledge, no studies have yet assessed its effect on the olfactory behaviour of *T. erytraeae*.

An important finding of our study is that although female *T. erytraeae* were attracted to *C. ladanifer*, this plant also exhibited the highest mortality rate among the aromatic species tested. This increased mortality may not be due to a lack of essential nutrients but rather to the exudates covering the plant. *Cistus ladanifer* secretes a significant amount of exudate (labdanum) on its leaves and photosynthetic stems (Sosa et al. 2005). Labdanum is rich in secondary metabolites, with 358 different compounds identified, including phenols, terpenes, alkaloids, polyacetylenes, fatty acids, and steroids (Sosa et al. 2005; Tena et al. 2021). According to our observations, once *T. erytraeae* settled on the plant, it became stuck in the exudates and could not free itself, leading to its death.

Lavandula stoechas and *F. vulgare* also attracted females *T. erytraeae*; however, none of the influential VOCs emitted by these aromatic plants showed a significant positive correlation with the insects' olfactory responses. Antwi-Agyakwa et al. (2019) reported that specific VOCs or blends in precise

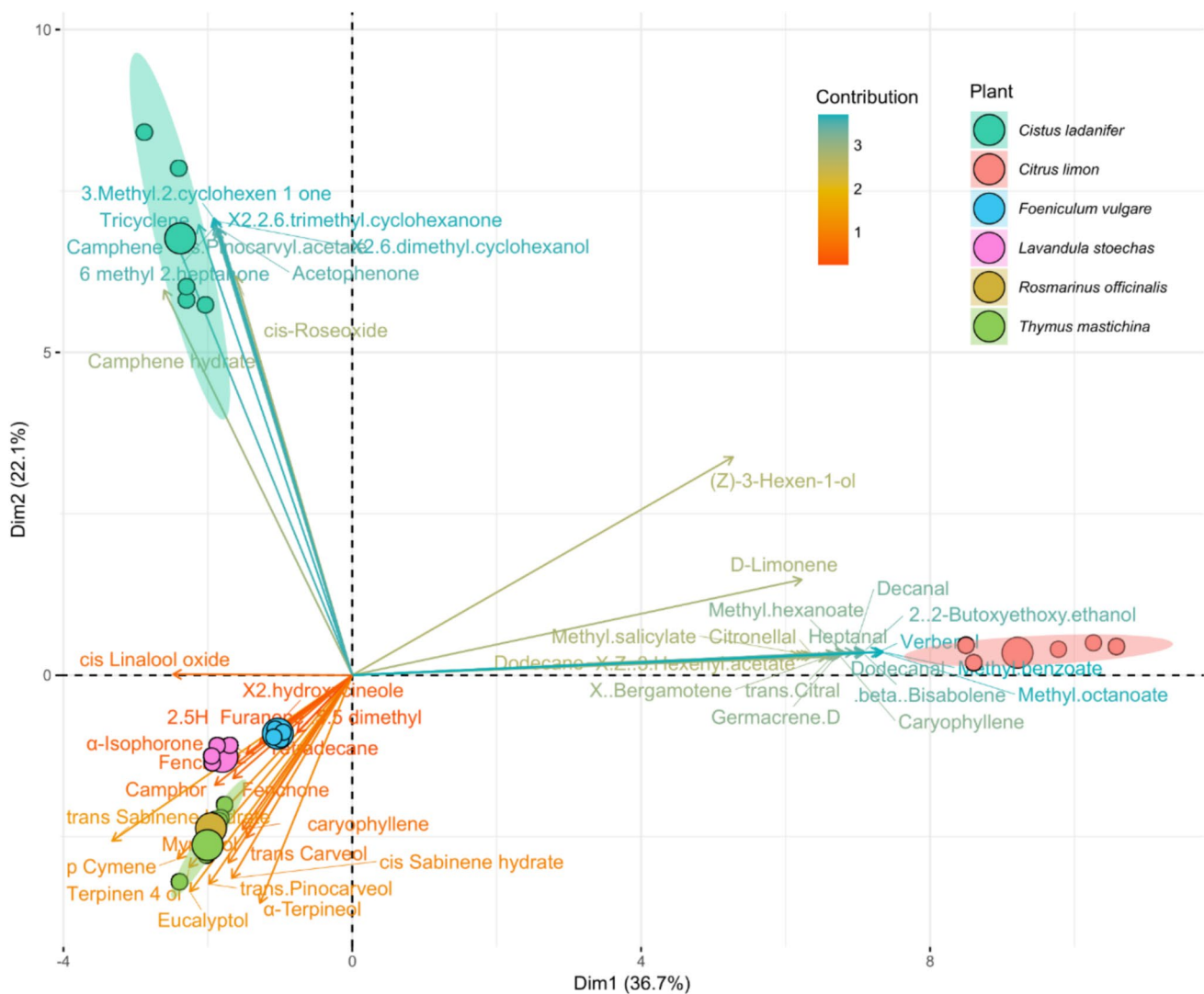


Fig. 4 Principal Component Analysis (PCA) biplot of the most influential VOCs affecting the olfactory response of *Trioza erytreae*, emitted by *Cistus ladanifer*, *Citrus limon*, *Foeniculum vulgare*, *Lavandula stoechas*, *Rosmarinus officinalis*, and *Thymus mastichina*

ratios play a crucial role in host plant location by *T. erytreae*. This suggests that the observed attraction may result from a synergistic effect of multiple VOCs rather than a single compound. Future research should focus on identifying the specific VOCs or combinations responsible for this attraction and determining their precise ratios and potential applications in pest management strategies.

In contrast, *T. mastichina* showed a significantly lower probability of attraction to female *T. erytreae* compared to *C. ladanifer*, *F. vulgare*, *L. stoechas*, and *C. limon*. The volatile profile of this plant was characterized by the presence of borneol, caryophyllene, myrtenol, and terpinen-4-ol. Importantly, these compounds were found to correlate negatively with the olfactory behavior of *T. erytreae*, suggesting they may actively contribute to a repellent response. Although these VOCs are also present in other aromatic plants, they

typically occur at lower concentrations and are always absent in *C. limon*. Previous research has reported that caryophyllene exhibits high repellent efficiency against *D. citri* (Alquézar et al. 2017; Li et al. 2024; Amorós et al. 2019). Regarding borneol, it is reported to possess repellent and toxic properties against mosquitoes (Nararak et al. 2020; Xu et al. 2023). Furthermore, myrtenol has been identified as a repellent for the pine beetle (*Dendroctonus armandi*) (Zhao et al. 2019), and terpinen-4-ol has shown significant insecticidal effects against stored-grain pests (Liao et al. 2019). However, the specific impacts of these compounds on psyllid species, such as *D. citri* and *T. erytreae*, remain unexplored.

In our study, males showed a significantly higher probability of attraction to *C. limon* than to *R. officinalis*, *T. mastichina*, and *L. stoechas*. This contrasts with previous observations by Benhadi-Marín et al. (2021) and Antwi-Agyakwa

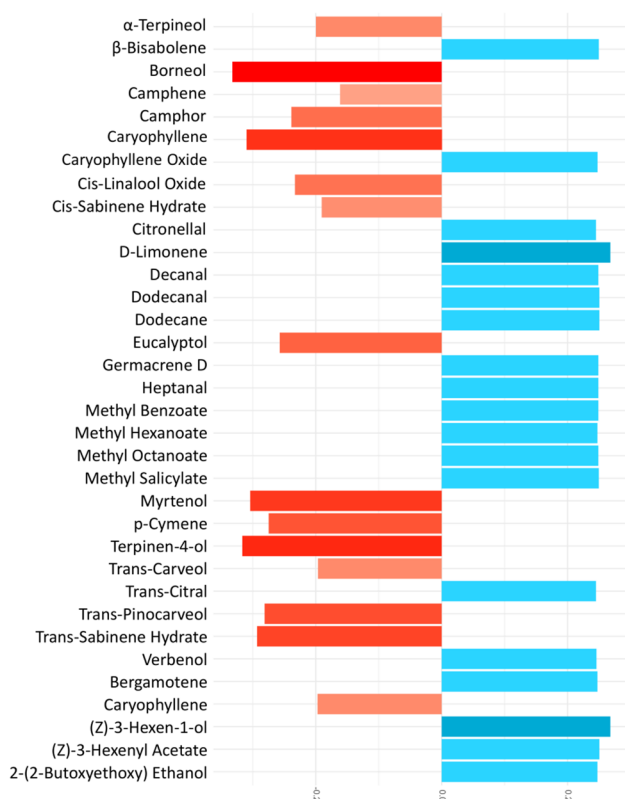


Fig. 5 Pearson correlation between the olfactory response of adults of *Trioza erytreae* and volatile organic compounds (VOCs) emitted by *Cistus ladanifer*, *Citrus limon*, *Foeniculum vulgare*, *Lavandula stoechas*, *Rosmarinus officinalis*, and *Thymus mastichina*. The analysis includes only VOCs preselected by the random forest model ($GIM \geq 2$), and only those showing statistically significant correlations ($p < 0.001$) are displayed ($n = 480$)

et al. (2019), which reported that *T. erytreae* males did not respond to lemon plants (*C. limon* and *C. gambhir*, respectively). Such differences may be attributed to variations in experimental protocols (e.g., differences in volatile concentrations, exposure durations, and environmental conditions) as well as inherent biological factors, including genetic variability and population-specific adaptations to *C. limon*. In contrast, female *T. erytreae* displayed a broader and more differentiated olfactory response than males, showing higher attraction probabilities to several plant species beyond *C. limon*. This broader responsiveness is consistent with the need of females to locate suitable host plants for oviposition, which likely requires finer discrimination among plant-derived olfactory cues (Van den Berg and Deacon 1989). Such sex-specific differences reinforce the importance of considering female-biased responses when evaluating plant volatiles involved in host selection and their potential application in pest management strategies.

Conclusion

Our study demonstrates that the tested plants have a significant impact on the survival and olfactory response of *T. erytreae*, with important implications for managing this pest in citrus orchards. *Citrus limon* was the preferred host plant, both in terms of survival and olfactory attraction, reinforcing the crucial role of its volatiles, such as D-limonene and (Z)-3-Hexen-1-ol, in host selection.

The aromatic plant *C. ladanifer* attracted female *T. erytreae* while also causing high mortality, likely due to its exudates. This dual effect makes it a promising candidate for further research as a trap plant to help control *T. erytreae* populations in citrus-growing areas. In contrast, *T. mastichina* exhibited the lowest probability of female attraction compared to *C. ladanifer*, *F. vulgare*, *C. limon*, and *L. stoechas*, probably due to the presence of borneol, caryophyllene, myrtenol, and terpinen-4-ol in its volatile profile, as these compounds showed a negative correlation with the olfactory response of the psyllids.

While these results highlight the potential of certain aromatic plants and their volatiles in integrated pest management strategies, it is important to note that these conclusions are based on laboratory assays. As such, further field studies are needed to validate these findings and evaluate their practical applicability in real-world conditions.

Author contributions

IR, JAP, AF conceptualized and designed the study. JBC, DR, and NR methodology collected the data. IR analyzed the data. JBC and IR writing – Original draft preparation. Review and editing: all authors contributed equally. All authors contributed to the study and gave final approval for publication.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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