UNIVERSIDAD AUTÓNOMA AGRARIA ANTONIO NARRO

SUBDIRECCIÓN DE POSGRADO

COMPUESTOS VOLÁTILES DE PLANTAS DE TOMATE Y SU EFECTO EN EL COMPORTAMIENTO DE *Bactericera cockerelli* Y SU PARASITOIDE *Tamarixia triozae*

Tesis

Que presenta JUAN MAYO HERNÁNDEZ

Como requisito parcial para obtener el Grado de
DOCTOR EN CIENCIAS EN PARASITOLOGÍA AGRÍCOLA

Saltillo, Coahuila   Junio 2019

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triozae*

Tesis

Elaborada por JUAN MAYO HERNÁNDEZ como requisito parcial para
obtener el grado de Doctor en Ciencias en Parasitología Agrícola
con la supervisión y aprobación del Comité de Asesoría

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Resumen

COMPUESTOS VOLÁTILES DE PLANTAS DE TOMATE Y SU EFECTO EN
EL COMPORTAMIENTO DE *Bactericera cockerelli* Y SU PARASITOIDE
Tamarixia triozae

POR

JUAN MAYO HERNÁNDEZ

DOCTOR EN CIENCIAS

EN PARASITOLOGÍA AGRÍCOLA

UNIVERSIDAD AUTÓNOMA AGRARIA ANTONIO NARRO

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Saltillo, Coahuila   Junio 2019

La interacción planta-insecto ha existido desde hace millones de años y ha sido estudiada ampliamente en los últimos años. Dichas interacciones han propiciado que las plantas hayan desarrollado numerosas estrategias para evitar el establecimiento y/o la alimentación de los insectos plaga, y la atracción de enemigos naturales como depredadores y parasitoides. El objetivo de esta investigación fue determinar cómo influye la planta hospedera en el crecimiento y desarrollo de *Bactericera cockerelli*, y la atracción de su parasitoide *Tamarixia triozae*. Además de identificar el perfil de los compuestos orgánicos volátiles que emiten cada una de las variedades utilizadas en el estudio (Floradade, Silvestre y Micro-Tom). Los resultados obtenidos en las pruebas de preferencia de oviposición (libre elección) mostraron que la variedad Floradade atrae significativamente mayor numero de adultos de *B. cockerelli* para su oviposición; de igual forma sobre esta variedad se obtuvo un mayor desarrollo de ninfas y adultos. Al evaluar el comportamiento de *T. triozae* en pruebas de libre elección de parasitismo sobre ninfas de tercer estadio de *B. cockerelli* alimentadas en las diferentes plantas hospederas utilizadas. Se encontró que *T. triozae* tiene preferencia por parasitar en plantas de la variedad Floradade con un 44% en comparación con las otras dos variedades. Las pruebas de olfatómetro mostraron que los adultos de *T. triozae* son más atraídos por las plantas dañadas por las ninfas de tercer estadio del psílido. En cuanto al ensayo con plantas sanas el parasitoide es más atraído por las variedades Floradade y Micro-Tom. En el perfil de compuestos volátiles en plantas libres e infestadas de ninfas de *B.cockerelli*, las variedades Floradade y Silvestre emitieron alrededor de 14 mientras que Micro-Tom emitio cinco. Entre los compuestos con mayor abundancia se encontraron: gamma.-Terpineno y β-Sabineno en Floradade; (+)-4-Careno, gamma-Terpineno, y β –Phellandreno en la variedad Silvestre y α-Pineno en Micro-Tom. El grado de domesticación en las plantas de tomate influyó en la atracción o repelencia, crecimiento y desarrollo de *B. cockerelli* y *T. triozae*. Así mismo los compuestos volátiles encontrados podrían estar involucrados en el efecto de atracción y/o repelencia de los insectos hacia las plantas.

Palabras clave: Floradade, Micro-Tom, Oviposición, Parasitismo, Silvestre.

Abstract

VOLATILE COMPOUNDS OF TOMATO PLANTS AND THEIR EFFECT ON BEHAVIOR OF *Bactericera cockerelli* AND ITS PARASITOID *Tamarixia triozae*

BY

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SCIENCES DOCTOR IN

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The plant-insect interaction has existed for millions of years and has been studied extensively in recent years. These interactions have shown that plants have developed strategies to avoid the establishment and/or insect pests feeding and the attraction of natural enemies as predators and parasitoids. Taking into account the aforementioned, the objective of this research was to determine how to influence the host plant on the growth and development of *Bactericera cockerelli* and the attraction of its natural enemy the parasitoid *Tamarixia triozae*. In addition to identifying the volatile organic compounds profile that emit each variety used in this study (Floradade, Wild and Micro-Tom). The outcomes obtained in preference tests (free choice) showed that Floradade variety attracted mostly adults of *B. cockerelli* for their oviposition. This same variety obtained a greater development of nymphs and adults of tomato psyllid. When evaluating *T. triozae* behavior in free choice tests on nymphs of third stage of *B. cockerelli* fed in the different host plants used. It was found that *T. triozae* preferred to parasitize on plants of Floradade variety by 44% compared to the other two varieties. Olfactometer tests showed that *T. triozae* adults were more attracted to damaged plants by the third stage of the psyllid. In the test with healthy plants, the parasitoid was more attracted by Floradade and Micro-Tom varieties. In volatile compounds profile in plants infested and free of *B.cockerelli* nymphs, Floradade emitted around 14 compounds in common as well as the Wild variety and Micro-Tom only emtitted five compounds. Among the compounds with greater abundance were: gamma.-Terpinene and β-Sabineno in Flroradade; (+) - 4-Careno, gamma-Terpinene and β –Fellandrene in Wild variety and α-Pinene in Micro-Tom. The domestication degree in tomato plants influences in the attraction or repellency, growth and development of *B. cockerelli* and *T. triozae*. Likewise, the volatile compounds influence the effect on the attraction or repellency of the insects towards the plants.

Keywords: Floradade, Micro-Tom, Oviposition, Parasitism, Wild.

INTRODUCCIÓN

Las plantas intactas emiten mezclas de compuestos orgánicos volátiles diferentes a las plantas, que responden al daño causado por la alimentación de insectos fitófagos que no solo difieren de manera cuantitativa y cualitativa. Estas mezclas complejas de compuestos volátiles, difieren en su composición, dependiendo de la naturaleza específica del organismo atacante. Algunas respuestas de las plantas al ataque de insectos fitófagos son usadas como señales por los depredadores y parasitoides de los de los herbívoros cuando buscan alimento (Dicke y van Loon, 2000). Se ha demostrado que los compuestos volátiles que liberan las plantas desempeñan un papel importante en la regulación del comportamiento de los enemigos naturales de los insectos plaga (Yang *et al.,* 2016). En algunos casos, en condiciones de campo los depredadores y parasitoides atraídos por los compuestos volátiles inducidos por los fitófagos aumentan las tasas de depredación y parasitismo y disminuyen los daños causados por los herbívoros (Heil, 2004; Karban, 2007). A la atracción de enemigos naturales de los insectos plaga se le considera una defensa indirecta de la planta, debido a que el comportamiento inducido de la planta provoca un cambio en el comportamiento del tercer nivel trófico (Karban, 2008). La calidad nutricional que la planta hospedera aporta al crecimiento y desarrollo de los herbívoros afecta también el desempeño de los depredadores y parasitoides en el tercer nivel trófico (Prager *et al*., 2014; Hernández-Moreno *et al*., 2017), al afectar la proporción de parasitismo, alimentación, sobrevivencia, proporción de hembras y machos y longevidad de su descendencia (Hernández-Moreno *et al.,* 2017). La efectividad del parasitismo o depredación de los enemigos naturales sobre las plagas varía dependiendo de las condiciones de manejo que se le dé al cultivo y el hábitat que rodee a los enemigos naturales (Bravo y López, 2007; Liu *et al.,* 2012; Trujillo-García *et al.,* 2018). La pérdida de genes de resistencia propiciados por el fitomejoramiento y el grado de domesticación de las plantas hospederas son factores importantes en la atracción de herbívoros y sus enemigos naturales (Stenberg *et al*., 2015; Li *et al.,* 2017). Por todo lo antes mencionado, los objetivos del presente trabajo se enfoncaron en identificar los compuestos

orgánicos volátiles de tres variedades de tomate, oviposición, crecimiento y desarrollo de *Bactericera cockerelli*, asimismo en la preferencia de parasitismo de *Tamarixia triozae* en ninfas desarrolladas en las variedades de tomate utilizadas en la investigación.

Objetivo general

> Identificar y cuantificar compuestos volátiles emitidos por plantas de tomate (*Solanum lycopersicum* L.) y su efecto en el comportamiento de *Bactericera cockerelli* y su parasitoide *Tamarixia triozae.*

Objetivos específicos

1. Determinar el perfil de compuestos volátiles emitidos y exclusivos de plantas de tomate infestadas y libres de *B. cockerelli.*

2. Identificar los compuestos volátiles en plantas de tomate infestadas y libres de *B. cockerelli.*

3. Documentar el comportamiento de *B. cockerelli* y *T. triozae* y su relación con volátiles emitidos por plantas de tomate.

Hipótesis

> La infestación de plantas de tomate (*Solanum lycopersicum* L.) con *Bactericera cockerelli* permitirá la liberación de compuestos volátiles como defensa y a su vez funcionarán como atrayentes de *Tamarixia triozae.*

REVISIÓN DE LITERATURA

El cultivo de tomate

El tomate *Solanum lycopersicum* L., denominado anteriormente como *Lycopersicum esculentum* Mill, pertenece a la familia Solanaceae. Es una planta herbácea anual, bianual, de origen centro y sudamericano. Actualmente es cosmopolita, se cultiva para consumo en fresco e industrializado (Allende, 2017). El cultivo ha logrado popularidad en los últimos años con el descubrimiento de la actividad antioxidante y anticancerígena del licopeno (Wu *et al.*, 2011; Raiola *et al.,* 2014). Por lo tanto, su producción y consumo se ha incrementado, llegando a ser el séptimo cultivo en importancia mundial con un área cultivada de 5.8 millones de hectáreas en el 2017 (FAOSTAT, 2019).

Debido a que *S. lycopersicum* es uno de los vegetales más cultivado en el mundo (500 variedades aproximadamente); para satisfacer la demanda se ha tenido que crear nuevas variedades y encontrar nuevos parientes silvestres que ayuden a crear las características agronómicas deseadas (Bredemeijer *et al.*, 2002; Sun *et al.,* 2014). Algunas variedades son destinadas para la siembra agrícola y unas más destinadas como modelos de investigación o utilizadas para realización de diferentes tipos de ensayos, como es el caso de las variedades que se mencionan a continuación.

Micro-Tom

La variedad "Micro-Tom" (Micro-Tomate) es una planta enana en miniatura que originalmente fue creada para la jardinería doméstica. Fue liberada por la Universidad de Florida en 1989 y desarrollada por el Dr. J.W. Scott y el Dr. B.K. Harbaugh (Scott y Harbaugh, 1989). Este cultivar fue propuesto como modelo de estudio por Meissner y colaboradores (1997) al cumplir con los requerimientos agronómicos, genéticos y moleculares. Su tamaño pequeño, su alta densidad por metro cuadrado (1,357 plantas m^2) y la producción de frutos y semillas dentro de un periodo de 70-90 días. Además, la variedad Micro-Tom se puede cultivar en laboratorio con mucha facilidad (Gratão *et al.,* 2008).

Floradade

La variedad "Flora-Dade" conocida también como Floradade es de crecimiento determinado, liberada en el año de 1976, desarrollada por la Universidad de Florida, se adapta muy bien a clima cálido. La planta es grande y con follaje abundante. Se seleccionó principalmente por su adaptación a los suelos calcáreos del sur de Florida. Es resistente a la marchitez causada por *Verticilium albo-atrum* y a *Fusarium oxysporum* f. *lycopersici* a las razas uno y dos, resistente a mancha gris en hojas causada por *Stemphylium solani.* La fruta es firme y se desprende de la planta con facilidad (Volin y Bryan, 1975).

Silvestre

En el año del 2015 se realizó una colecta de material vegetal y frutos de una variedad silvestre de tomate en el bajío Guanajuatense con el propósito de empearla como modelo de estudio en interacciones con insectos plaga. Esta planta es arbustiva, es escasa en la región, es considerada como maleza y sus frutos sirven de alimento para ganado y algunas aves; crece hasta 1.6 metros de alto y 1.2 metros de ancho, sus frutos son de tamaño muy pequeño (1.5 cm). Esta variedad silvestre fue caracterizada en 2016 por taxónomos del Instituto de Ecologia A.C. (INECOL) de Xalapa, Veracruz; siendo catalogada como *Solanum lycopersicum*.

Enfermedades y plagas del tomate

Como en todos los cultivos su rendimiento se ve afectado por el ataque de enfermedades y plagas. De acuerdo a Agrios (2005), Bernal (2010) y Ruiz *et al.,* (2011) entre las enfermedades y plagas mas importantes se encuentran:

Damping off

Este complejo de hongos (*Pythium* spp., *Rhizoctonia solani*, *Phytophthora* sp, *Fusarium* sp) es muy común. Provoca el ahorcamiento del cuello y pudrición de la raíz de la plántula ocasionando marchitamiento y posteriormente la muerte. Las plántulas se entristecen como si les faltara agua, empieza por plantas aisladas que después se extienden en manchones.

Pudrición radicular

Esta enfermedad es causada por *Fusarium oxysporum*. En plantas adultas comienza con un amarillamiento de las hojas viejas que después se extiende a todas las hojas de la planta, se marchitan y mueren adheridas al tallo. Al realizarse un corte transversal se puede observar necrosis de color café rojizo en forma de anillo, la cual se extiende hacia arriba de acuerdo con la severidad. Las plantas muestran un achaparramiento, defoliación, necrosis marginal de las hojas y finalmente la planta muere.

Marchitez por *Verticillium*

Al igual que *Fusarium*, *Verticillium dahliae* ataca los haces vasculares y provoca marchitez, pero la diferencia es que al hacer el corte transversal el anillo es de color gris, en las hojas se forma un alo amarillo en forma de "V" y se presenta en condiciones más templadas, además de que forma pequeños esclerocios.

Moho gris

Causado por *Botrytis cinerea*. Infecta en cualquier etapa de desarrollo, inclusive durante el transporte y almacenamiento del fruto. En hojas, tallos y flores produce tizones con presencia de un polvo grisáceo color café en forma irregular y anillos concéntricos. Sobre el fruto se presentan manchas circulares con los bordes blancos, después ocurre una necrosis de color café-rojiza y se cubre del polvo grisáceo.

Tizón tardío

Esta enfermedad causada por *Phytophthora infestans* ataca todos los tejidos aéreos de la planta. En las hojas se caracteriza por la aparición de manchas irregulares de tamaño variable, son de color verde oscuro con los márgenes pálidos, los cuales con alta humedad desarrollan esporulación blanquecina, posteriormente se vuelven de color café y pueden invadir la lámina foliar haciendo que el peciolo se doble hacia abajo, los frutos dañados presentan grandes manchas color café-rojizo.

Tizón temprano

Los síntomas causados por el tizón temprano (*Alternaria alternata*) se presenta inicialmente en hojas viejas del cultivo en forma de lesiones irregulares de color café oscuro, en cuyo interior se forman anillos concéntricos los cuales son rodeados de un halo amarillo como consecuencia de la reacción del tejido sano a una toxina liberada por el desarrollo del hongo. Al avanzar la infección se forman puntos negros abultados. *A. alternata* también ataca flores, frutos, plántulas y la parte basal de los tallos.

Cenicilla polvorienta

Los síntomas de la cenicilla polvorienta causada por *Leveillula taurica* aparecen como un polvo color blanco en el haz y envés de las hojas más viejas de la planta, en condiciones óptimas con una alta presencia de inoculo puede atacar también las hojas jóvenes. Aparecen manchas de color amarillo en el haz de las hojas, donde el hongo se reproduce y libera nuevas esporas, las cuales van a continuar infectando las hojas sanas. Un ataque severo de cenicilla polvorienta vuelve las hojas cloróticas con los bordes enrollados y se quedan adheridas al tallo de la planta, provocando un debilitamiento y deshidratación de la planta por lo que los frutos no crecen, quedan sin sabor y son afectados por el sol por la ausencia de tejido foliar que pueda protegerlos.

Permanente del tomate

Esta enfermedad es transmitida por el psílido *B. cockerelli*, al alimentarse directamente del floema. En las hojas se observa una clorosis en los bordes de los foliolos en la parte apical de las plantas infectadas. Provoca un achaparramiento de la planta y enroscamiento de las hojas jóvenes en el haz, adoptando colores verde pálido o amarillo. Provoca aborto de flores, debido a que las flores se secan. Los frutos se reducen en cantidad y tamaño y no sufren deformaciones. Hasta la fecha no se ha probado su transmisión mecánicamente, ni por semilla. Esta enfermedad puede presentarse en cualquier etapa de desarrollo del cultivo.

Mosquita blanca

Se puede encontrar *Trialeurodes vaporariorum* y/o *Bemisia tabaci*. La importancia de esta plaga radica en su rápida reproducción en corto tiempo. Su alimentación provoca un debilitamiento, amarillamiento, moteado y contaminación de hojas y frutos por la excreción de mielecilla.

Trips

Los trips (*Thrips tabaci* y *Frankliniella occidentalis*) provocan daño directo al alimentarse, ya que raspan la superficie de las hojas lo que ocasiona que la planta no realice la fotosíntesis adecuadamente, se deshidrate y puedan entrar enfermedades. Los trips son vectores de virus como el de la "Marchitez Manchada del Tomate" e "Impatiens Necrotic Spot Virus".

Pulgón

Los pulgones (*Myzus persicae*) al igual que los trips ocasionan daños directos al succionar la savia provocando debilitamiento, pérdida de vigor, amarillamiento y deformaciones, excretan mielecilla la cual cubre las hojas ocasionando la atracción de moscas y hormiga, así como del hongo *Capnodium* sp (fumagina) que reduce la fotosíntesis y calidad de los frutos. Los pulgones son vectores del virus del mosaico de la alfalfa, el virus del ápice amarillo del tomate y el virus del mosaico del pepino.

Araña roja

Tetranychus urticae ocasiona severos daños al cultivo de tomate al cubrir la planta con telaraña. Altas temperaturas y un ambiente seco son ideales para el desarrollo de esta plaga. Los adultos como las ninfas se alimentan al absorber la savia de las hojas, provocando puntuaciones blancas, coloraciones amarillentas y marrones en las hojas. Poblaciones altas de araña roja llegan a ocasionar la defoliación total de las plantas.

Gusano del fruto

Las larvas de los dos primeros instares del gusano del fruto *Heliothis* (=*Helicoverpa*) *zea* se alimentan de follaje de la planta y conforme se van desarrollando llegan a dañar los frutos en formación. Presentan seis estados larvales de colores variables con una franja oscura con micro espinas (pináculos) en el dorso dividido por una línea clara.

Bactericera cockerelli

Bactericera cockerelli Sulc., es una plaga de importancia económica ya que se ha reportado un rango de hospederos de 40 especies en 20 familias, teniendo preferencia por la familia solanácea (Pletsch, 1947; Wallis, 1951; Butler y Trumble, 2012). Entre las que sobresalen papa (*Solanum tuberosum*), chile (*Capsicum annuum*), tomate (*Solanum lycopersicum*) y berenjena (*Solanum melongena*). La importancia de este insecto radica que al alimentarse acumula gotas de miel que da como resultado un moho que interfiere con la fotosíntesis y puede contaminar el fruto. Al alimentarse del floema de las plantas hospederas causa una enfermedad llamada "el amarillamiento del psílido" (Butler y Trumble, 2012), además de que transmite la bacteria "*Candidatus* Liberibacter solanacearum" ("*Candidatus* Liberibacter psyllaurous") (Hansen *et al*., 2008; Crosslin y Munyaneza, 2009; Liefting *et al.,* 2009).

Clasificación taxonómica

La clasificación taxonómica de acuerdo al CABI (2019)

Dominio: Eukaryota

Reino: Metazoa

Phylum: Arthropoda

Subphylum: Uniramia

Clase: Hexapoda

Orden: Hemiptera

Suborden: Sternorrhyncha

Superfamilia: Psylloidea

Familia: Triozidae

Género: Bactericera

Especie: *Bactericera cockerelli* Sulc.

Ciclo de vida

El ciclo de *B. cockerelli* está conformado por huevecillos, cinco estados ninfales y adulto (Marín *et al.,* 1995). El ciclo de vida de huevecillo a adulto en condiciones normales varía de 20-26 días, pero esto dependerá de las temperaturas a las que se exponga, así como de la planta en la cual se desarrolle (Xiang-Bing y Tong-Xian, 2009).

Distribución

Se ha reportado la presencia de *B. cockerelli* en países de Centroamérica como El Salvador, Honduras, Nicaragua y Guatemala. En Norteamérica se reporta en algunos estados de Canadá y algunos estados de Estados Unidos de América. En México se ha reportado en los estados de México, Nuevo León, Coahuila, Tlaxcala, Sonora, Oaxaca, San Luis Potosí, Michoacán,

Durango, Baja California, Morelos, Puebla, Guanajuato, Nayarit y Sinaloa. También se ha documentado su presencia en Nueva Zelanda (Rubio-Covarrubias *et al.*, 2006; Teulon *et al.*, 2009; CABI, 2019).

Control de *Bactericera cockerelli*

El control de *B. cockerelli* se basa principalmente en el uso de insecticidas químicos sintéticos como thiacloprid, imidacloprid, abamectina, esfenvalerate, β-cyflutrin, clotianidin, spirotetramat, espiromesifen, tiametoxan, spinetoram, oxamil entre otros. Las malas aplicaciones y el uso irracional de estos ingredientes activos han conducido a la aparición de resistencia del psílido a los insecticidas químicos, por lo que se han estado buscando implementar nuevas estrategias para el control de este insecto. Entre las alternativas para controlar *B. cockerelli* se encuentran el uso de extractos naturales, uso de *T. triozae* como biológico y la disrupción del ambiente del insecto (Rubio-Covarrubias *et al.,* 2006; Yang *et al.,* 2010; Dávila-Medina *et al.,* 2012).

Tamarixia triozae

Es una avispa ectoparasitoide sinovigénica (Himenoptera: Eulophidae) que parasita ninfas de *B. cockerelli* de tercer, cuarto y quinto instar (Rojas *et al.*, 2015). Aparece de forma natural en México y en el suroeste de Estados Unidos (Lomeli-Flores y Bueno, 2002). Al ser un ectoparasitoide sinovigénico se alimenta de ninfas de su huésped, esto le confiere ventaja como agente de control biológico, ya que elimina ninfas de *B. cockerelli* por oviposición y depredación (Cerón-González *et al.,* 2014).

Clasificación taxonómica

De acuerdo a Boucek (1998) según La Salle (1994) la reclasifica y reconoce como sigue:

Reino: Animal

Phyllum: Arthropoda

Clase: Hexapoda

Orden: Hymenoptera

Superfamilia: Chalcidoidea

Familia: Eulophidade

Subfamilia: Tetrastichinae

Género: *Tamarixia*

Especie: *T. triozae* (Burks, 1943)

Ciclo de vida

El ciclo de vida de *T. triozae* de huevecillo hasta la emergencia de adultos es de aproximadamente de 12 días a 26°C. Los huevecillos, larvas y pupas duran 1.5, 3.5 y 5.7 días respectivamente; las hembras adultas viven 19.9 días y su periodo de preoviposición es aproximadamente de 1.9 días (Rojas *et al.,* 2015).

***Tamarixia triozae* como agente de control biológico**

El potencial de *T. triozae* como agente de control biológico sobre ninfas de *B. cockerelli* se ha estudiado recientemente (Luna-Cruz *et al*., 2015), por ser un importante ectoparasitoide sinovigénico que se alimenta de los tres últimos estadios ninfales de *B. cockerelli* (Rojas *et al.,* 2015). Esta característica le confiere ventaja como agente de control biológico al eliminar las ninfas del psílido por oviposición y depredación (Cerón-González *et al.,* 2014). El parasitismo de *T. triozae* puede variar entre el 5 y 95% dependiendo de las

condiciones de manejo que se le dé al cultivo, como la aplicación de insecticidas y el hábitat que rodee al parasitoide (Bravo y López, 2007; Liu *et al.,* 2012; Trujillo-García *et al.,* 2018). Una hembra de *T. triozae* es capaz de matar a 300 ninfas entre parasitismo y su alimentación (Cerón-Gonzalez *et al.,* 2014).

¿Qué son los compuestos orgánicos volátiles?

Los compuestos orgánicos volátiles (COV) son un gran grupo de productos químicos constituidos fundamentalmente por carbono con bajo peso molecular y alta presión de vapor. Estos compuestos se dispersan con gran facilidad cuando entran en contacto con el medio ambiente. La mayoría de los volátiles son producidos por organismos vivos como parte de sus procesos metabólicos (Bennet y Inamdar, 2015). Los compuestos volátiles emitidos por las plantas son metabolitos de bajo peso molecular <300 Da y con un bajo punto de ebullición <260°C. Estos compuestos pueden ser emitidos por diferentes partes de la planta como pueden ser flores, hojas, frutos y raíces, permitiendo a la planta interactuar con otros organismos (Negre-Zakharov *et al.,* 2009).

Liberación de compuestos volátiles por las plantas

Muchos de los compuestos volátiles de las plantas son liberados a través de las membranas de los tejidos epidérmicos, donde se sintetizan, o de otras estructuras, como los tricomas, osmóforos (estructuras especializadas en la producción de aromas, generalmente se encuentran en las flores) o células epidérmicas crenuladas que se encuentran comúnmente en las partes de las flores que se especializan en la liberación de compuestos. En hojas y tallos, los volátiles también se liberan por los poros a través de los cuales el CO_2 se asimila. La apertura y cierre de estomas también influye en la liberación de compuestos volátiles. Algunos volátiles se almacenan en la vacuola, los cuales son considerados como precursores cuando el tejido es dañado por los herbívoros (Baldwin, 2010).

Los compuestos volátiles emitidos de las partes vegetativas de la planta, están involucrados en muchos tipos de interacción biótica. Cuando los herbívoros (insectos principalmente) atacan a las plantas, estas son sometidas a un daño mecánico y los insectos liberan algunos elicitores, los cuales inducen una serie de eventos en las plantas. Varios de los elicitores derivados por la alimentación del insecto han sido identificados que inducen la emisión de compuestos volátiles, tales como conjugados de aminoácidos (Alborn *et al.,* 1997; Bonaventure *et al.,* 2011), β-glucosidasa (Mattiacci *et al.,* 1995), inceptinas (Schmelz *et al.,* 2006), caeliferinas (Alborn *et al.,* 2007) y un componente lábil al calor no identificado (Allmann y Baldwin, 2010). Estos elicitores reportados se han identificado en insectos masticadores, mientras que en insectos chupadores los elicitores que inducen la emisión de compuestos volátiles no se han reportado aun, ya que no es fácil determinar cantidades de elicitores de residuos pequeños en los insectos chupadores. Tentativamente se ha encontrado β-glucosidasa en la chicharrita café del arroz (*Nilaparvata lugens*), la cual se ha propuesto como un elicitor potencial en la emisión de compuestos volátiles en el arroz (Du *et al.,* 2005).

Función de los compuestos volátiles

Se conoce que los compuestos volátiles están involucrados en varios tipos de interacción biótica y abiotica; especialmente los isoprenoides que juegan un papel importante y relativamente apreciado en respuesta a estrés de tipo abiótico (Vickers *et al.,* 2009). Otra función conocida de los COVs es crear una defensa directa contra los herbívoros o patógenos. Muchos reportes indican que los compuestos volátiles emitidos por la planta pueden actuar como repelentes de herbívoros. Por ejemplo, los volátiles de hojas verdes (VHV) pueden ayudar a la planta a tener una resistencia contra herbívoros y hongos fitopatógenos (Shiojiri *et al.,* 2006). Las mezclas de monoterpenos, sesquiterpenos o VHV impiden la oviposición de algunas hembras de especies de lepidóptera (Holopainen y Gershenzon, 2010).

La señalización dentro de la planta y la interacción planta-planta es otra función que se le atribuyen a los compuestos volátiles. La comunicación que se da con las plantas vecinas ha sido tema de discusión por varios años. Se han realizado investigaciones donde las plantas responden a la señal de los compuestos emitidos por plantas vecinas atacadas por herbívoros (Baldwin *et al.,* 2006). La controversia que hay sobre la interacción planta-planta, ha estimulado a la realización de otro tipo de investigaciones con respecto a la señalización dentro de la planta en diferentes órganos.

Los compuestos volátiles juegan un papel importante en la atracción de enemigos naturales (depredadores y parasitoides) de los herbívoros. Las plantas los atraen para poder defenderse de sus ataques. En plantas transgénicas de *Arabidopsis* los compuestos terpenoides específicos y los compuestos volátiles de hojas verdes lograron la atracción de enemigos naturales de la palomilla de la col (*Pieris rapae*) (Shiojiri *et al.,* 2006; Schnee *et al.,* 2006).

Los compuestos volátiles en las interacciones tritróficas

El papel que desempeñan los compuestos volátiles en las interacciónes tróficas es de suma importancia. Tal y como ha quedado demostrado en más de 23 especies de plantas en combinación con su herbívoro y su enemigo natural (Dicke, 1999). Entre los ejemplos más estudiados se encuentra la interacción de la haba (*Phaseolus lunatus*), su fitófago *Tetranychus urticae* y su depredador *Phytoseiulus persimilis*. Similar al daño que causan los insectos fitófagos cuando se alimentan, la oviposición también es detectada por las plantas, lo cual induce una emisión de compuestos volátiles los cuales atraerán parasitoides de los huevecillos (Hilker y Meiners, 2002). Esto sucede poco después de la oviposición, permitiéndole a la planta defenderse antes de que ocurra el daño, es decir antes de que los huevecillos eclosionen (Hilker *et al.,* 2002).

La mezcla de volátiles que emiten las plantas es muy diversa, tanto de forma cuantitativa y cualitativa, lo que dificulta conocer al compuesto responsable de la atracción. Se ha sugerido realizar pruebas de manera individual con cada compuesto encontrado en la interacción planta-plaga-parasitoide/depredador. Encontrando por ejemplo que la atracción de *P. persimilis* se debe a la presencia del alcohol (3S)- (*E*)-nerolidol (Kappers *et al.,* 2005). Mientras que para la atracción de *Cotesia marginiventris*, un parasitoide generalista de larvas de la familia noctuidae se necesita de la liberación de (*E*)-*β*-farnesene y (*E*)-α-bergamoteno principalmente (Schnee *et al.,* 2006).

Bactericera cockerelli Sulc[1] Oviposition Preference and Development on Three Tomato Varieties

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Abstract. Interactions between plants and insects have been widely studied. Plants develop numerous strategies to avoid establishment and/or feeding by insects. The aim of this research was to evaluate oviposition preference, nymphal development, and survival of *Bactericera cockerelli* Sulc on 'Floradade', 'Micro-Tom', and 'Wild' varieties of tomato (*Solanum lycopersicum* L.). Free-choice assays showed *B. cockerelli* oviposited twice more on 'Floradade' than 'Micro-Tom' with 1,000 and 479 eggs, respectively. Nymphal stages as well as adults of the pest developed much better on Floradade' variety to emerge 3 days earlier than in 'Micro-Tom' and 'Wild' varieties. Adult emergence percentage was 52, 36, and 18% for 'Floradade', 'Micro-Tom', and 'Wild'. Results in a greenhouse showed the degree of domestication of tomato varieties affected oviposition preference and survival of the insect.

Introduction

Volatile organic compounds that create smell of a plant can affect insects on plants (Dudareva et al. 2006). Plants produce specific blends of volatile organic compounds in response to insect attack and pathogenic or beneficial microorganisms (Janssen et al. 2002, Arimura et al. 2005, Bautista-Lozada and Espinosa-Garcia 2013, Sharifi et al. 2017). Blends of volatile organic compounds induced by herbivores can prevent future attack in plants (Bautista-Lozada and Espinosa-Garcia 2013, Sharifi et al. 2017) or attract natural enemies of pest insects (Rashid et al. 2012). Defense compounds produced by plants in response to damage affects feeding, oviposition, growth, and survival of herbivorous insects (Dudareva et al. 2006, Arimura et al. 2009, Rashid et al. 2012). However, choice mechanisms in an insect to a host plant are not always established because of generality of some insect pests to feed and/or develop (Price et al. 2011). Many factors determine the host range of an herbivore, including ability to detect a host, physiology of the larval/nymphal stage, natural enemies, and reproductive behavior (Crawley 1983, Bernays 2001, Bernays and Grahm 2013, Forister and Wilson 2013), as well as plant

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nutritional quality, that help insects survive (Nanthagopal and Uthamasamy 1989). Other factors influencing oviposition preference are insect dispersion and proximity of another host plant (Mayhew 1997, Scheirs et al. 2000, Scheirs and De Bruyn 2000, Janz 2005). Some insect species have few hosts such as a single genus or family. This is not true for *Bactericera cockerelli* Sulc that has a host range of 40 species in 20 families but prefers the Solanaceae family (Pletsch 1947, Wallis 1951, Butler and Trumble 2012). *B. cockerelli* is an economically important pest in solanaceous crops such as potato (*Solanum tuberosum* L.), pepper (*Capsicum annuum* L.), tomato (*Solanum lycopersicum* L.), and eggplant (*Solanum melongena* L.) because of: 1) honeydew accumulation that results in mold that interferes with photosynthesis and contaminates fruit; 2) feeding on host plant phloem causing "yellowing psyllid" disease; and 3) as a vector of "*Candidatus* Liberibacter solanacearum" ("*C.* L. psyllaurous") (Crosslin and Munyaneza 2009, Hansen et al. 2009, Liefting et al. 2009). Oviposition preference and behavioral differences of the pest were evaluated on three varieties of tomato with different degrees of domestication: 'Floradade', 'Micro-Tom,' and 'Wild.' Development and survival of *B. cockerelli* nymphs to adults were studied. Free-choice assays were used to determine oviposition preference. Eggs were monitored to determine how many eggs and nymphs reached the adult stage on the varieties used as hosts. *B. cockerelli* was more attracted for oviposition to the Floradade variety that provided conditions necessary for development to adulthood of the insect.

Materials and Methods

Low-tech conditions in a greenhouse at Centro de Investigación en Química Aplicada at Saltillo, Coahuila, México were used for the study. A colony of *B. cockerelli* (infected with "*Candidatus* Liberibacter solanacearum") was provided by the Molecular Laboratory of Parasitology Department of Universidad Autónoma Agraria Antonio Narro. *B. cockerelli* adults were reared on plants of 'Agata' potato. Seeds of three tomato varieties were provided by the Research Center at Centro de Investigación en Química Aplicada. The psyllid colony and different plant varieties were reared at 28 ± 2°C in a greenhouse.

Once seeds germinated, 25-day-old tomato seedlings were transplanted into a 2:1 mixture of peat moss and perlite in 1.5-liter plastic pots, irrigated three times a week with 25% Steiner nutrient solution, and assayed 15 days after transplanting. Three plants of each tomato variety were put into a 50 x 50 x 50-cm wooden cage covered with organza fabric, and 250 *B.*

cockerelli adults were released into the cage for 96 hours. The insects were removed, and eggs were counted (according to Prager et al. 2014). Plants were inspected daily to determine the number of hatched eggs, small nymphs (first and second instars), large nymphs (third, fourth, and fifth instars), and emergence of adults that were removed immediately from the plants. Nymphal stages were determined by the size of the body or presence of wing pads (Liu and Trumble 2006). The assay ended when all adults finished emerging from all infested plants.

The experimental design was completely randomized with four replications. Means were compared by Tukey's test ($P = 0.05$) using the SAS statistical package (SAS Institute 2002).

Results

In a choice assay experiment, *B. cockerelli* preferred to oviposit on the Floradade variety ($P < 0.0001$) where most eggs were laid, followed by Micro-Tom and Wild varieties (Fig. 1). Oviposition on Floradade was on the entire plant, the adaxial part, and the underside of the leaf. Eggs were on the middle of Micro-Tom plants and on medium and low strata of Wild plants. On Micro-Tom and Wild varieties, oviposition was only on the upper side of leaves, indicating that *B. cockerelli* preferred to oviposit on Floradade and to a lesser degree on Micro-Tom and Wild plants.

Most 1st-instar nymphs ($P < 0.001$) hatched from eggs (N1) on Floradade compared with Wild or Micro-Tom tomato plants, with statistical differences between the last two varieties (Fig. 2). Eggs laid on Floradade hatched 3 days before those on Wild or Micro-Tom plants. This suggested that Floradade tomato plants successfully influenced hatching of *B. cockerelli* eggs. This might be caused by egg quality from nutritional differences between host plants.

Free-choice assay of all nymphal stages from egg hatching to emergence of adults was used to evaluate survival of *B. cockerelli* on different tomato varieties. Data were analyzed statistically for each nymphal stage of *B. cockerelli*. The analyses indicated significant effect on each nymphal stage; $P = 0.0003$ for second instar, $P = 0.0001$ for third and fourth instars, $P = 0.0008$ for fifth instar, and $P = 0.005$ for the adult stage. *B. cockerelli* nymphs on Floradade developed to the adult stage faster than did nymphs on Wild or Micro-Tom plants on which adults emerged 3 days later. All nymphal stages of *B. cockerelli* developed well on Floradade, followed by Micro-Tom. On the Wild variety, fewer nymphs developed, although in the adult stage, no statistical difference was found with the Micro-Tom variety (Fig.2). In plants of Wild and Micro-Tom varieties, some fourth- and fifth-instar nymphs died and appeared dry which was not observed on Floradade. Dead nymphs were cultured on potato dextrose agar culture to eliminate entomopathogenic microorganisms (data not shown). After 1 week, no growth was found on the culture medium.
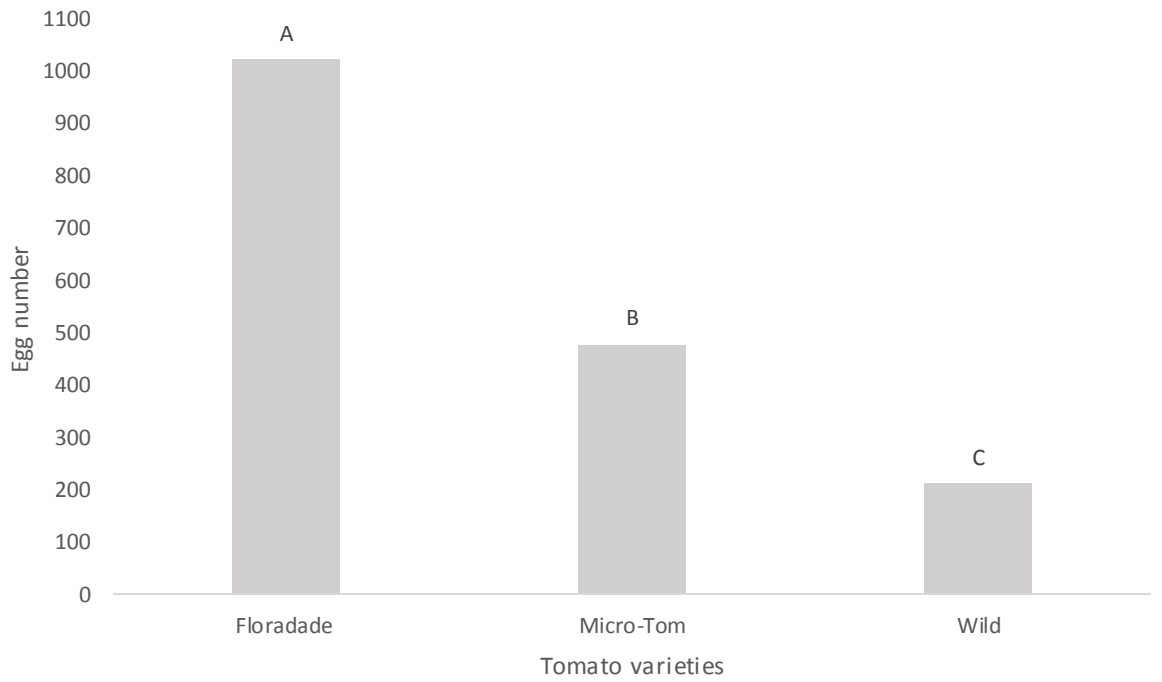
Fig. 1. Number of eggs laid by *B. cockerelli* on three tomato varieties during 96 hours in choice assays. Different letters indicate statistical difference (*P* = 0.05).
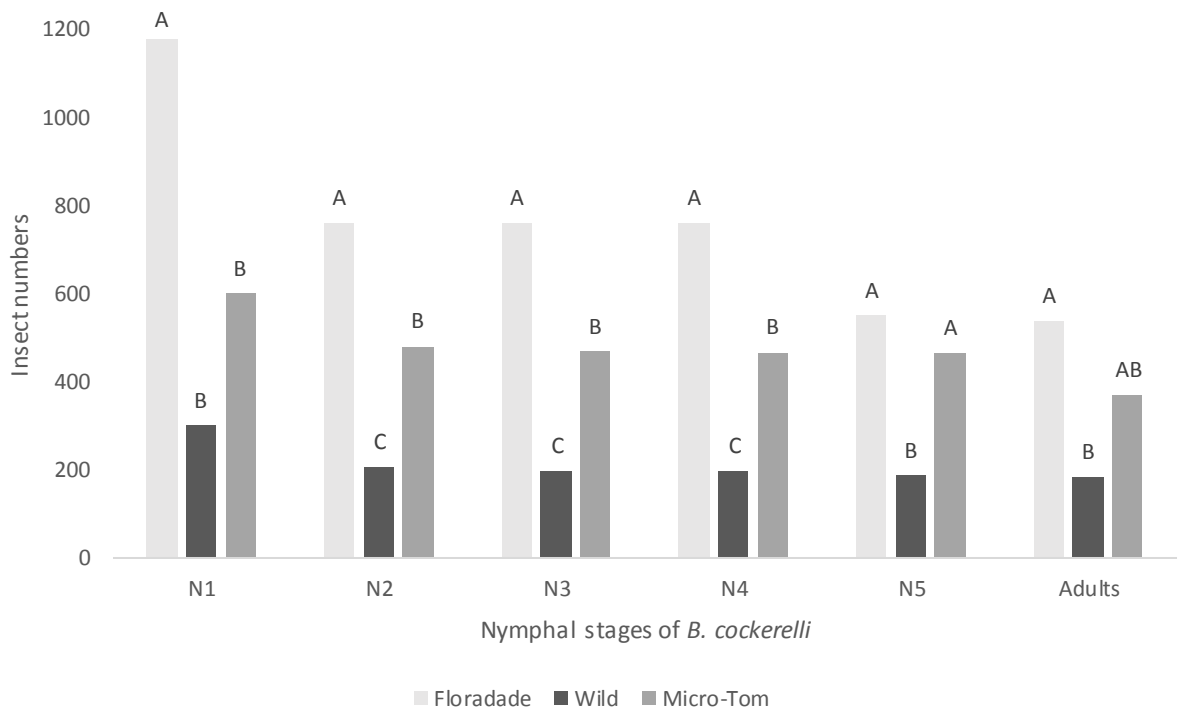

Fig. 2. Average number of *B. cockerelli* nymphal stages that survived on three tomato varieties. Bars with different letters are statistically different (*P* = 0.05).

Discussion

B. cockerelli preferred Floradade plants for oviposition. Kariyat et al. (2013) mentioned that volatile organic compounds emitted by plants were key for feeding and oviposition by insect pests as well as their natural enemies. However, Li et al. (2017) attributed oviposition preference to the degree of domestication of a plant. A more domesticated plant attracts more insects to oviposit, indicating that domesticated plants emit different compounds than do less domesticated plants; such compounds attract insects. The events can be explained as "gene erosion" by plant breeding, being the main cause of susceptibility of commercial varieties to insect pests and diseases (Stenberg et al. 2015). Floradade plants were larger in size and foliar area compared to Wild and Micro-Tom varieties, which might influence attraction by *B. cockerelli* because plants with greater leaf coverage tend to attract more insects (Thinakaran et al. 2015). *B. cockerelli* adults with an ovipositing option prefer more domesticated plants because the degree of susceptibility to attack is greater compared with less domesticated plants (Liu and Trumble 2004, 2005, 2006).

According to results of the study, egg hatching and nymphal development are because insects prefer plant species that help growth and development, avoiding those that do not provide optimal conditions, although a plant species can be suitable for feeding, but might not provide optimal nutrition for nymphal development (Prager et al. 2014). Least nymphal development on plants of Wild and Micro-Tom varieties was because when plants detect insects feeding on them, they activate genes that encode for resistance proteins, inhibiting growth and development of larvae or nymphs (Casteel et al. 2006). The dead nymphs of fourth and fifth stages on Wild and Micro-Tom varieties might be attributed to secondary metabolites produced by the plants before feeding by *B. cockerelli* nymphs. Among secondary metabolites produced by plants attacked by insects are phenolic compounds and flavonoids that have an antifeedant effect for insects, tannins that affect growth and development through production of resistance proteins that reduce nutrient absorption causing lesions in the midgut of an insect, producing an astringent taste in the sap, acting as a deterrent to the pest (Rashid et al. 2012).

In conclusion, free-choice assays indicated definite oviposition preference by *B. cockerelli* for the Floradade variety. The variety provided the conditions necessary for nymphs to achieve favorable development of the life cycle. Wild and Micro-Tom varieties that probably produce defensive metabolites that inhibit insect growth did not allow proper development of nymphs. This study provided information on behavior of the tomato/potato psyllid on domesticated varieties of tomatoes.

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Artículo 2

Tamarixia triozae response on *Bactericera cockerelli* developed in three tomato varieties

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Abstract The *Bactericera cockerelli* (Sulc) (Hemiptera:Triozidae) psyllid is vector of "*Candidatus* Liberibacter solanacearum" bacterium, that causes diseases in solanaceae, and can reduce production up to 80%. The pest control is based on use of synthetic chemical insecticides, plant extracts and natural enemies such as the parasitoid *Tamarixia triozae* (Burks) (Hymenoptera:Eulophidae). *T. triozae* feeds on nymphs of third, fourth and fifth instars of *B. cockerelli*, reaching up to 95% of parasitism, depending the crop management and the type of host the pest. The aim of this work was to evaluate the parasitic behavior of *T. triozae* on *B. cockerelli* nymphs fed on Floradade, Wild and Micro-Tom tomato varieties, and identify the parasitoid attraction towards uninfested plants (healthy) and infested plants (damaged) of said varieties. Parasitism preference tests and "Y" tube olfactometer tests were performed respectively. The parasitism tests showed that *T. triozae*

prefers to parasitize on plants of Floradade variety by 44% in comparison with the other two varieties (P <0.0003). *T. triozae* was more attracted to damaged plants by N3 nymphs of *B. cockerelli* of Wild variety (P = 0.0523). Healthy plants of Floradade and Micro-Tom varieties attracted a higher proportion of parasitoid, except in Wild variety, where *T. triozae* was more attracted to damaged plants. The domestication degree in tomato plants influenced positively by attracting *T. triozae* to a greater extent.

Keywords Domestication, Floradade, Micro-Tom, Parasitism, Preference, Wild

Introduction

The potato/tomato psyllid *Bactericera cockerelli* (Sulc) (Hemiptera:Triozidae) has become one of the most important pests from the economic point of view in solanaceae crops such as: potato (*Solanum tuberosum* L.), pepper (*Capsicum annuum* L.), tomato (*Solanum lycopersicum* L.) and eggplant (*Solanum melongena* L.) (Butler and Trumble 2012), due to its type of diet and because it is the vector of "*Candidatus* Liberibacter solanacearum" bacterium (Hansen et al. 2008; Liefting et al. 2009). Between the years 2006 and 2008, yield losses of more than 20% were reported, equivalent to 33.4 million dollars per year because of this bacterium (CNAS 2006; Wen et al. 2009; Munyaneza 2012). Its control is based mainly on the use of synthetic chemical insecticides and plant extracts as repellents (Yang et al. 2010). For biological control of *B. cockerelli*, several natural enemies have been reported, among which *Tamarixia triozae* (Burks) (Hymenoptera: Eulophidae) parasitoid stands out

(Morales et al. 2013; Rojas et al. 2015). The *T. triozae* potential for the potato/tomato psyllid regulation has recently been studied (Luna-Cruz et al. 2015), this being an important ectoparasitoid that feeds on nymphs of third, fouth and fifth stage of *B. cockerelli* (Rojas et al. 2015). This feature gives it an advantage as a biological control agent by eliminating the psyllid nymphs by oviposition and predation (Cerón-González et al. 2014). The *T. triozae* parasitism on *B. cockerelli* nymphs can vary between 5 and 95% depending on the management conditions given to the crop and the habitat surrounding the parasitoid (Bravo and López 2007; Liu et al. 2012; Trujillo-García et al. 2018). The *B. cockerelli* populations regulation by *T. triozae* is affected by multiple factors, such as the lack of alternate hosts, the asynchrony of host and parasitoid, the size of the sown fields that limits the dispersal capacity, the synthetic insecticides aplication and the presence of hyperparasitoids (Butler and Trumble 2011; Liu et al. 2012). The reduction of parasitoid abundance is also affected by the domestication degree of plant, by emitting a different range of volatile compounds that affect the parasitism and parasitoid feeding behavior (Halitschke et al. 2008). The emission of these volatile compounds can help or affect the natural enemy in its decision speed towards its prey (Li et al. 2017). The parasitoid performance is influenced by the host plant origin by affecting the parasitism proportion, feeding, survival, females proportion and longevity of their offspring (Hernández-Moreno et al. 2017). The aim of this study was to evaluate the parasitic behavior of *T. triozae* on *B. cockerelli* nymphs in Floradade, Wild and Micro-Tom tomato varieties, as well as to observe their attraction in healthy plants and infested plants of these varieties. It was observed that *T. triozae* in a higher proportion prefers N3 nymphs fed

on plants of Floradade variety, in this same variety the adult emergence of parasitoid was advanced three days. In olfactometer test, *T. triozae* adults chose a higher proportion of damaged plants of Wild variety.

Materials and Methods

Experiment location. The present work was carried out in the municipality of Saltillo, Coahuila, within the facilities of Centro de Investigación en Química Aplicada (CIQA) under low-tech greenhouse conditions.

***Bactericera cockerelli**.* The *Bactericera cockerelli* colony was provided by the Molecular Parasitology Laboratory of Parasitology Department of Universidad Agraria Autónoma Antonio Narro. The *B. cockerelli* adults were reared in potato plants (*Solanum tuberosum*) Ágata variety. The psyllid colony was kept under greenhouse conditions at 28°C ± 2°C in a wooden cage of 60 x 80 x 80 cm with anti-aphid mesh.

Tamarixia triozae. The parasitoids were acquired in "Koppert Biological Systems-Mexico" company, located in state of Querétaro México.

Seedtime. The three tomato varieties seeds were provided by Dr. José Humberto Valenzuela Soto of Department of Plastics in Agriculture from CIQA. Once the seeds were germinated, the 25-day-old seedlings were transplanted in plastic pots with 1.5 L capacity with peat moss and perlite mixture in a 2:1 ratio, and were watered three times a week with Steiner nutrient solution at 25%. Subsequently, 15 days after transplantation, they were used for bioassays. The plants were kept under greenhouse conditions at 28°C ± 2°C.

Parasitism preference. In a greenhouse, three plants of Floradade, Wild and Micro-Tom tomato varieties were placed inside a 50 x 50 x 50 cm wooden cage, covered with organza fabric. In each cage 250 non-sexed adults of *B. cockerelli* were released for 72 h, after this time the insects were removed and the eggs placed in each plants were counted. This assay was replicated twice. The eggs hatched and development was allowed until the nymphs passed to third nymphal stage (N3) and at this time *T. triozae* adults were released for 24 hours, to parasitize the nymphs, then *T. triozae* adults were removed. After 14 days, the *T. triozae* adults emergence in parasitized nymphs in each plants used in the assay were counted.

Olfactometer assay. Y-shaped glass tube olfactometers were used to determine the *T. triozae* attraction preference towards infested and free plants of *B. cockerelli* nymphs N3 in the three tomato varieties. The olfactometers were 1.3 cm in diameter, 12 cm in length from the base of the tube to the union of the "Y" arms and 13 cm in length of the arms spaced at 45° (Díaz-Montano and Trumble 2012).

The first part of assay consisted using plants of three varieties infested with nymphs N3 of *B. cockerelli* and placing them in a desiccator with an air source so that this would drag the aromas. An activated charcoal filter was placed between the air source and the desiccator, to remove impurities from the air. The air was allowed to circulate for 10 minutes before introducing the corresponding plant into the desiccator, five minutes after placing the plants, 40 parasitoids were placed at the end where the desiccator air exited. Their behavior was observed for 10 minutes. It was taken as an attraction when *T. triozae* adults crossed two centimeters from the arm of Y tube. Three

repetitions were performed separately, using 100 parasitoids in total. The plants combinations were: Floradade vs Wild, Floradade vs Micro-Tom and Wild vs Micro-Tom. The second part of assay consisted of placing plants the same variety infested and free of nymphs N3 of *B. cockerelli* in the desiccator. The procedure was the same as mentioned above. The assay was performed for each variety.

Statistical analysis

The experiments were established under a completely random design, the data collected were transformed, which were later used to perform an ANOVA. When was necessary, the comparison between means was made using a Tukey multiple range test ($P = 0.05$). Statistical analyzes were made using statistical package SAS 9.0 version.

Results

When *B. cockerelli* was released in three tomato varieties, so that they had the option to oviposit. It was found that the psyllid oviposited more times in domesticated variety (Floradade) with 367 ovipositions on average per plant, 2.6 and 2.4 times more than in the variety Wild and Micro-Tom respectively, varieties with less domestication degree. The statistical analysis shows a significant difference of $P < 0.005$ to Floradade variety with respect to the variety Wild and Micro-Tom to have the highest number of ovipositions, while Wild and Micro-Tom varieties are equal statistically to obtain an average of ovipositions of 141 and 150 respectively (Fig. 1).
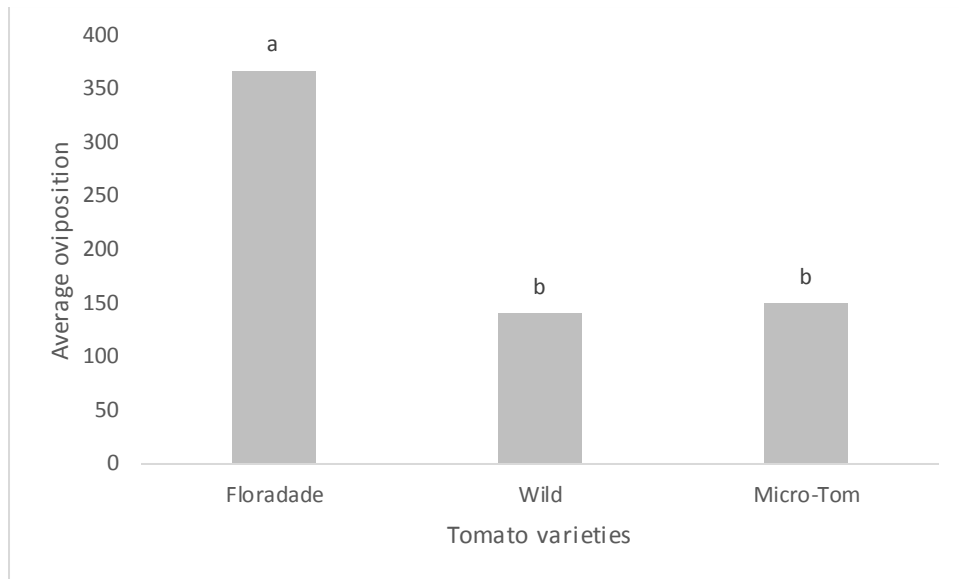
Fig.1 Number of eggs of *B. cockerelli* in tomato plants of three varieties. Different letters indicate statistical differences ($P = 0.05$).

In parasitism assay, the proportion of parasitized nymphs N3 differed among the three varieties. The parasitism percentage in Floradade was 44.6%, followed by Wild and Micro-Tom with 23.1 and 1.8%. *T. triozae* parasitized in greater percentage in domesticated plants than in plants of the variety Wild and Micro-Tom, plants with a lower domestication degree (Fig. 2). The emergence of *T. triozae* adults in Floradade plants occurred at 11 days after the parasitoid was removed, while in Wild and Micro-Tom varieties the emergence was after 14 days. The statistical analysis shows a significant difference of parasitism of $P < 0.0003$ among the different varieties.
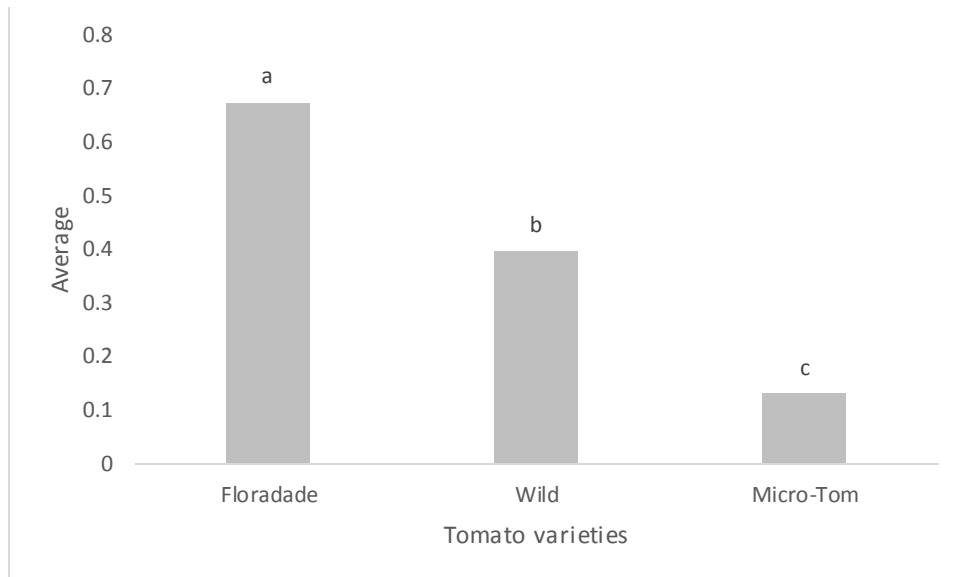
Fig. 2 Average nymphs of *B. cockerelli* parasitized by *T. triozae* in different tomato varieties. Different letters indicate statistical differences ($P = 0.05$).

When the attraction preference in Y tube of *T. triozae* was directly compared in plants of different varieties infested with nymphs N3 of *B. cockerelli*. The Wild variety showed a greater attraction of the parasitoid with a mean 0.23, followed by the most domesticated variety Floradade and Micro-Tom with an average of 0.17 and 0.10 respectively (Fig. 3). The statistical analysis shows significant difference ($P = 0.0523$) in three varieties used.
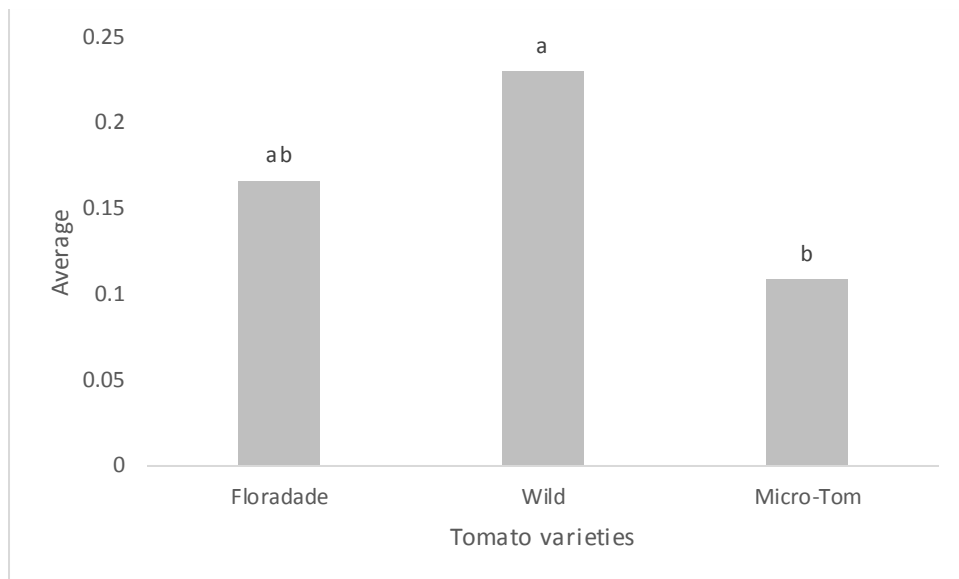
Fig. 3 Average of *T. triozae* adults attracted in infested plants with nymphs N3 of *B. cockerelli* in different tomato varieties. Different letters indicate statistical differences ($P = 0.05$).

Olfactometer tests (Y-tube) showed that N3-free plants were more attractive compared to plants infested with nymphs N3. Except in plants of Wild variety, where the parasitoids were more attracted by the damaged plants. In plants free of nymphs N3 of *B. cockerelli*, the attraction of *T. triozae* was more significant in Floradade and Micro-Tom varieties with an average of 0.3 and 0.29, the Wild variety showed less attraction of *T. triozae* adults with a average of 0.14 respectively (Fig. 4). The statistical analysis shows that Floradade and Micro-Tom varieties are equal to each other and different from the Wild variety with a significant difference of $P = 0.0127$.
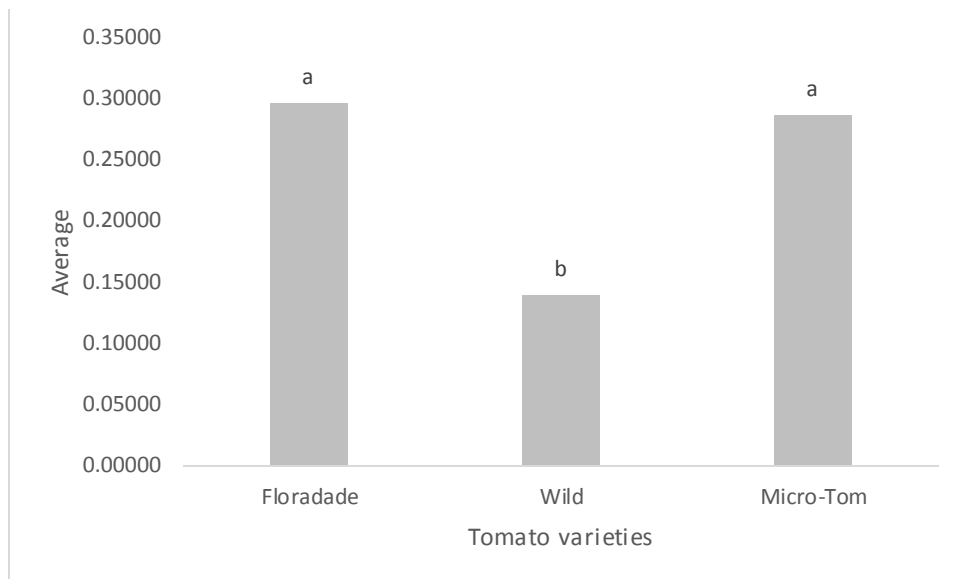
Fig. 4 Average of *T. triozae* adults attracted in plants free of nymphs N3 *of B. cockerelli* in different tomato varieties. Different letters indicate statistical differences (*P* = 0.05).

Discussion

It was found that Floradade variety had a greater number of ovipositions of *B. cockerelli* compared to the less domesticated ones: Wild and Micro-Tom. The amount of eggs deposited in different varieties may be due to factors of the plant itself such as plant size, leaf color, glandular trichomes presence, nutritional quality and volatile compounds released, these factors affect the insects decision to oviposit (Williams III et al. 2012). The volatile compounds production from domesticated plants is different to the compounds of wild plants (Li et al. 2017), which implies a greater or lesser attraction of insect pests. The *T. triozae* parasitism had significant differences in the three varieties. Floradade obtained the highest percentage of parasitized N3 nymphs and the lowest Micro-Tom percentage. The parasitism percentage in Wild variety was intermediate compared to the other two varieties. These results differ with those found by Li et al. (2017), where they reported that

Cotesia congregata, the parasitoid of *Manduca sexta* was more attracted to wild tomato plants than domesticated tomato plants. They attribute this preference to release of different volatile compounds emitted by plants. Hernández-Moreno et al. (2017) found that in tritrophic interactions the first level affects the performance of the third trophic level, by showing that *T. triozae* originally bred in chili plants had 3% more parasitism than adults raised in tomato plants. These same authors mention that by better understanding the interaction of Solanaceae-*Bactericera cockerelli-Tamarixia triozae* model, the control of the pest can be optimized by taking advantage of the positive influences on parasitoid performance. Salas-Araiza et al. (2014) found that parasitism was higher in jalapeño pepper plants compared to potato and tomato plants, thus demonstrating that the host affects in the third trophic level. Regarding to emergence time adults of *T. triozae*, in Floradade variety they emerged at 11 days after having been parasitized the N3 nymphs, while in Wild and Micro-Tom varieties the emergence of adults was at 14 days. The advance of three days of emergency in Floradade plants can be used in favor to Integrated Pest Management (IPM). An important factor in the emergency advance may be the availability of nutrients in *B. cockerelli* nymphs, which accelerates the parasitoide growth and development. In laboratory conditions it was found that adults of *T. triozae* emergence was at 12 days in fourth and fifth instar nymphs of *B. cockerelli* fed on tomato plants (Rojas et al. 2015). When *T. triozae* preference was directly compared in damaged plants of the three varieties, a greater proportion of the parasitoids chose Wild plants instead of the domesticated varieties (Floradade and Micro-Tom). The volatile compounds production is an important mediator in attraction of parasitoid and

pest (Li et al. 2017). These same authors mention that the volatile compounds production of domesticated plants is different from those of wild plants, having an ecologically important implication in the attraction of natural enemies of the pests. In olfactometer test (Y-tube) where *T. triozae* and infested plants of the same variety were used versus N3-free plants. The parasitoids preferred N3-free plants than the plants infested with N3 nymphs in a large proportion, except in plants of Wild variety where the parasitoids preferred more infested plants than N3-free plants. The varieties domestication in Floradade and Micro-Tom could have influenced positively for *T. triozae* attraction before the arrival of *B. cockerelli*, not influencing negatively as mentioned by Li et al. (2017). The parasitoide attraction in damaged plants of Wild variety could be attributed to volatile compounds emission, which are responsible for recruiting *T. triozae* when the plant is attacked by *B. cockerelli.* The domestication degree in plants does not always have a negative influence on natural enemies attraction. Of the varieties used in this work, it was found that Floradade variety was the one with the highest percentage of parasitized nymphs, demonstrating that domestication have influenced in a positive way to attract the natural enemy of *B. cockerelli.* The use of this variety can be recommended to cultivate and release *T. triozae* when *B. cockerelli* is presence in the crop.

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Artículo 3

Changes in volatile organic compounds emissions by three tomato cultivars as response to psyllid (*Bactericera cockerelli* Sulc.) infestation

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Abstract

Tomato (*Solanum lycopersicum* L.) domesticated crops has been presented an increased susceptibility to pest under field and greenhouse conditions. Among these pests, tomato/potato psyllid (*Bactericera cockerelli* Sulc), is an important pest in solanaceous crops. In this study, volatiles organic compounds (VOCs) emissions from headspace in three healthy varieties of tomato plants (Floradade, Micro-Tom and Wild) were evaluated under greenhouse conditions and determined using solid phase microextraction and gas chromatography-mass spectrometry (SPME/GC-MS). Later, independent bioassays were performed to evaluate VOCs emissions with three varieties infested with nymphs of *B. cockerelli*. Results in healthy plants showed markedly differences of VOCs profile from each variety (21 compounds for Wild, 20 for Floradade and 3 for Micro-Tom). Floradade and Wild plants infested with nymphs showed changes in VOCs emissions distinctly. We could suggest that qualitative differences in VOCs profile by degree of domestication could explain the preferences by *B. cockerelli*.

Introduction

Crops interact with many organisms, which included phytopathogens and insect herbivores. Plant defenses involve different mechanism to avoid this attack, among direct defense we found salicylic acid (SA) pathway that is activated during plant-bacteria hemibiotrophic and phloem-feeding insects interactions (De Vos et al., 2005; Zarate et al., 2007); meanwhile, jasmonic acid/ethylene (JA/ET) pathway is activated by necrotrophic pathogens and chewing insects attack (Kessler and Baldwin, 2002; Glazebrook, 2005). In addition, plant defenses involved indirect mechanisms to counteract the damage caused by pathogens and herbivores (Erb 2018), and they are mediated by volatiles organic compounds (VOCs) with different plant functions.

Sometimes, plant defenses are not sufficient in crops, this represent a disadvantage because its reduced capacity to respond efficiently to biotic stress compared with wild relative plants (Guo et al., 2013). Wild tomato relatives produce abundant VOCs related-defense compared with domesticated varieties (Lundgren et al., 1985), other study demonstrated that domesticated tomato reduced the attracting of predators mediated by VOCs compared with wild relatives (Li et al., 2017). The VOCs released by wild tomatoes are less attractive and can repel the pest (tobacco whitefly) compared with domesticated tomatoes (Bleeker et al., 2009).

Under field and greenhouse conditions, tomato crops (*Solanum lycopersicum* L.) are often exposed to phytophagous insects that impairs the crop development and reduces the yields. The tomato psyllid, *Bactericera cockerelli* Sulc (Hemiptera: Triozidae) is considered as an important pest in Southeast USA and Northeast Mexico, attacking solanacaeous crops mainly in tomato and potato (*Solanum tuberosum* L.) (List 1939; Pletsch 1947; Wallis 1955). In North America and New Zealand, *B. cockerelli* is able to transmit the phloem-obligated proteobacteria *Candidatus* Liberibacter

solanacearum (CaLso) (Munyaneza 2012). CaLso in potato crops caused loss of more than $25 million between 2003 and 2005 in Texas (CNAS 2006; Munyaneza 2012). However, regarding tomato defense, CaLso induced early responses (1 week) and was mediated by SA, JA and ET signaling pathways, meanwhile, late responses (2 and 4 weeks) were downregulated of photosynthesis associated genes and genes involved in carbohydrate metabolism were upregulated (Huot et al., 2018). In agreement with Casteel et al., (2012), inoculation of CaLso in the absence of its vector host suppressed accumulation of defense transcripts (PR1 and AOS mRNAs), these results suggest that pathogens manipulates plant defenses to benefit themselves.

To explore the feeding behavior of the *B. cockerelli* on tomato plants many factors are required to host plant choice (Prager et al., 2014). Tomato plants respond differentially to herbivore damage by *B. cockerelli*, VOCs emissions between healthy plants and nymphs feeding of *B. cockerelli* shown several changes markedly in the blends emitted by the evaluated plants (Bautista-Lozada and Espinosa-García 2013). The VOCs emissions from healthy tomato plants also constitutes an important signal for psyllids preference, for example, in free-choice assays performed with *B. cockerelli* adults in three varieties of tomato, domesticated plants markedly increased *B. cockerelli* oviposition and a minor degree in Micro-Tom and Wild varieties (Mayo-Hernández, et al., 2018).

In this study, we evaluated the VOCs profiles emitted by three varieties of tomato plants (*Solanum lycopersicum* cv. Floradade, *S. lycopersicum* cv. Micro-Tom and *S. lycopersicum* cv. Wild), before and after nymphs feeding by *B. cockerelli*. Changes in VOCs emission were detected by HS-SPME-GCMS system during tomato-*B. cockerelli* interactions. Here we found some compounds that might be involved in the

B. cockerelli performance on tomato and this could be attributed either repellence or attraction of psyllids in field crops.

 Material and methods

Plant growth.

Tomato seeds (*Solanum lycopersicum*) from three varieties were germinated in peat-moss until two-leaf were presented. Seedlings from domesticated (*S. lycopersicum* cv. Floradade, CrownSeeds, USA), Micro-Tom (*S. lycopersicum* cv. Micro-Tom) and wild type (*S. lycopersicum* cv. Wild) were transplanted in 1.5 l pots containing peat-moss:perlite (70:30 v/v). Plants were watered each third day and fertilized once a week with a Steiner's nutritive solution (25%). Tomato plants were maintained under greenhouse conditions at 28°C ± 2 °C, RH=45% and were growing until reached at 20 cm of high or four to five fully extended leaves for the bioassays.

Insect rearing.

The potato/tomato psyllids (*Bactericera cockerelli* Sulc) were reared on tomato plants under greenhouse conditions. *B. cockerelli* (CaLso positive) was maintained in cages of 50 x 50 x 50 cm with the same conditions described above. Psyllids were donated by Departamento de Parasitología of Universidad Autónoma Agraria Antonio Narro (UAAAN), in Saltillo, Mexico.

Headspace collection and analysis of plant volatiles.

Three varieties of tomato plants (two weeks after transplanting) were selected to collect the volatile emissions (healthy plants). First, to obtain volatile profiles was employed the Headspace-Solid Phase Microextraction-Gas chromatography-mass spectrometry system (HS-SPME-GCMS), individual plants were placed into

polypropylene desiccator previously adapted with a charcoal activated trap and the flow-air was passed over the plant for five minutes (Floradade); polyethylene bags (Sunbag, SIGMA) were utilized for Micro-Tom and Wild. To obtain VOC profile, each treatment was evaluated for at least three-times on healthy tomato plants (free-psyllids).

To evaluate the released VOCs on three varieties during *B. cockerelli* nymph feeding, two bioassays were independently performed. With a small brush were gently collocated per plant, 25 nymphs of *B. cockerelli* (4th and 5th stages) and were left for 2 hours feeding on tomato leaves. After feeding, individual plants were collocated either bags or desiccator to evaluate head-space of each treatment by SPME. For SPME gray fiber (50/30 μm, DVB/CAR/PDMS, SUPELCO) was used in all evaluations, the fiber was exposed during 2.5 hours. Healthy plants (nymphs-free) were exposed at the same time for SMPE. The bioassays were performed at 28°C ± 2 under greenhouse conditions.

All fibers were injected and desorbed in a gas chromatograph (Agilent Technologies GC 7890A) coupled to mass selective detector (Agilent Technologies MSD 5975 C); all analysis were performed under the follow running conditions: oven temperature initial of 60°C during 1 min, increasing 8°C/min until 280°C for 1 min. Injector temperature was 230°C. The VOCs were analyzed employing a capillary column Agilent Technologies HP-5MS (30m x 250 um x 0.25 um). After 15 min, the fiber was removed from injector and stored until use.

Results

The profile of VOCs collected from headspace in three different varieties of tomatoes (healthy plants) qualitatively were detected and identified twenty-one VOCs for Wild, twenty VOCs in Floradade and three VOCs presented in Micro-Tom (Table 1). Among Floradade and Wild varieties, eleven compounds were shared in the VOCs blend: α-pinene, (+)-4-carene, ɣ-terpinene, α-terpinolene, ascaridole, δ-elemene, (-)-cis-β-elemene, isocariophyllene, caryophyllene, Bicyclo[7.2.0]undecane, 10,10-dimethyl-2,6-bis(methylene)-, [1S-(1R*,9S*)]- and humulene (Table 1, Figure 1). Micro-Tom presented a low emission of VOCs in healthy plants, only three compounds were detected: α-pinene, L-β-pinene and β-pinene (Table 1).

In Floradade, only five abundant compounds were detected in healthy leaves, such as o-cymene, (+)-4-carene, α-thujene, ɣ-terpinene and caryophyllene (Table 1). Wild relatives showed four abundant compounds such as (+)-4-carene, (+)-2-carene, (-)-α-pinene and ɣ-terpinene (Table 1). Micro-Tom only two abundant compounds were detected: α-pinene and L-β-pinene (lesser than Floradade and Wild) (Table 1).

However, when the three varieties of tomato were infested with nymphs of *B. cockerelli,* changes in VOC profiles emitted among varieties was evident. The Floradade-infested leaves released a blend of volatiles that includes: o-cymene, (+)-4-carene, ɣ-terpinene, (+)-2-carene, α-phellandrene, α-thujene, β-sabinene, δ-elemene, caryophyllene, humulene, 2,6-bis(1,1-dimethylethyl)-4-(1-oxopropyl)phenol and phenol, 2,6-bis(1,1-dimethylethyl)-4-(1-methylpropyl) (Table 2). In Wild-infested leaves were detected: α-pinene, 1,3,5-cycloheptatriene, 3,7,7-trimethyl, (+)-4-carene, α-terpinolene, ɣ-terpinene, (+)-2-carene, β-phellandrene, β-sabinene, δ-elemene, caryophyllene and humulene (Table 2). Micro-Tom showed four volatiles emitted in

response to nymph feeding, among these compounds were: α-pinene, β-pinene, caryophyllene and tetradecane (Table 2).

In Floradade-*B. cockerelli* interaction, (+)-4-carene, α-thujene, β-sabinene and caryophyllene were the most abundant VOCs and emitted in response to nymph feeding; meanwhile in Wild-*B. cockerelli* interaction, (+)-4-carene, α-terpinolene, β-phellandrene, and caryophyllene were the most abundant in emission; and α-pinene and β-pinene were the most abundant in Micro-Tom infested after 2 hours of herbivory on tomato leaves (Table 2).

To compare those compounds that are shared in three varieties of tomato (healthy), the figure 1 shows the eleven VOCs and their changes in level among varieties. For Wild and Floradade, (+)-4-carene and ɣ-terpinene results as major compounds emitted in plants free-psyllid (Figure 1). Those plants that were infested with psyllid showed eight similar VOCs, (+)-4-carene and β-sabinene were the most abundant among three varieties (Figure 2).

The three varieties of tomato plants emitted qualitative and quantitative changes in VOC emissions. For example, Floradade plants presented seven compounds and the majority of these compounds were in low amounts in infested plants (Figure 3). Wild plants with ten compounds, some of them with reduced abundance (Figure 4). Micro-Tom plants presented very poor emissions in all assay performed (Figure 5).

Discussion

In this study were evaluated VOCs emissions of three varieties of tomato in healthy and psyllid-infested plants. Previous study in our research group found that *B. cockerelli* adults presented a strong oviposition preference toward the domesticated *S. lycopersicum* cv. Floradade and a lesser degree in *S. lycopersicum* cv. Micro-Tom and

S. lycopersicum cv. Wild (Mayo-Hernández et al., 2018). These differences in psyllid preference could be attributed to VOCs blends in healthy plants, for this purpose, we performed some bioassays and the VOCs profile were obtained in healthy plants (Table 1). The qualitative differences among varieties of tomato VOCs suggest that some volatiles could act as attractant or repellent for *B. cockerelli* adults, although in this study an electroantennography analysis was not performed to validate theses results. In similar studies, healthy tomato plants (*S. lycopersicum* cv. Castlemart) emitted eleven VOCs in the constitutive blend, among these compounds we found α-pinene, o-cymene, (+)-4-carene and β-phellandrene (Bautista-Lozada and Espinosa-García 2013). These compounds shared with VOCs pattern from headspace of healthy tomato plants obtained from three varieties, although in the present study triggered twenty-one VOCs for Wild, twenty VOCs in Floradade and three VOCs presented in Micro-Tom (Table 1). The oviposition behavior by *B. cockerelli* in solanaceous crops is mediated for olfactory and visual stimuli to locate their hosts (Thinakaran et al., 2015); factors such as natal host plant and plant phenology also improve settling and oviposition (Prager et al., 2014). In other studies, wild varieties of tomato (*Solanum peruvianum*) that bearing *Mi-1.2* gene presented a reduced oviposition of *B. cockerelli* compared than susceptible varieties that lacking the gene (Casteel et al., 2006). In field conditions, *B. cockerelli* showed a strong preference for potato and tomato compared with eggplant and pepper (Thinakaran et al., 2015).

To determine if nymphs feeding of *B. cockerelli* promoted differences in VOCs emissions in three varieties of tomato, two bioassays of herbivory were performed on tomato leaves. The VOCs induced by nymphs on Floradade leaves showed two abundant compounds: α-thujene and β-sabinene (Table 2), VOCs induced in Wild plants were α-terpinolene and β-phellandrene as abundant (Table 2). Interestingly,

Micro-Tom plants infested with nymphs presented reduced number of VOCs emitted and α-pinene was the most abundant (Table 2). Although our experiments were performed with *B. cockerelli* CaLso-positive, two hours of herbivory by nymphs (4th and 5th stages) is sufficient to induce VOCs emissions for leaf damage. In this sense, CaLso could manipulated host tomato defenses within one week, when the pathogen population is increased in the phloem can evoked changes in expression of defense genes (Hout et. al. 2018) and this modification of gene expression may induce changes in VOCs emissions to attract the psyllid vector (Mas et al., 2014). Therefore, it was speculating that the changes in VOCs emission is attributed by herbivory of *B. cockerelli* for each tomato varieties.

Among plant responses to *Bactericera cockerelli* (free CaLso) involved the up-regulation of defense genes expression, WRKY and ERF transcription factors were activated during adult feeding on tomato plants; although nymph feeding triggered up-regulation of expression of hypersensitive response genes and those genes involved in photosynthesis were down-regulated (Hout et. al. 2018). This report confirm that tomato plants respond in different ways to psyllid infestation in different life stages, these differences could be attributed to specific elicitors delivered by each instar stage and could be produced in oral secretions during psyllid feeding on leaves damaged (Casteel, et al. 2012).

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Declaration of interest statement.

The authors disclaimed any conflict of interest.

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Tables

	VOCs	RT	Wild	Floradade	Micro-Tom
1	α-Pinene	4.574	++	++	++
2	o-Cymene	5.157		+++	
3	1,3,5-Cycloheptatriene, 3,7,7-trimethyl-	5.232	++		
4	L-β-Pinene	5.275			++
5	β-Pinene	5.344			+
6	(+)-2-P-Menthene	5.395	++		
7	(+)-4-Carene	5.631	++++	++++	
8	α-thujene	5.692		+++	
9	(+)-2-Carene	5.921	+++		
10	(-)-α-pinene	5.925	+++		
11	β-Phellandrene	6.166	++++		
12	γ-Terpinene	6.654	++	++++	
13	α-terpinolene	7.232	++	++	
14	Ascaridole	10.389	++	++	
15	δ-elemene	11.526	++	++	
16	Copaene	12.207		++	
17	(-)-Cis-β-elemene	12.469	++	++	
18	Isocaryophyllene	12.719	++	++	
19	2-Methyladamantane	12.79		+	
20	Alloaromadendrene	12.79		+	
21	Caryophyllene	12.917	++	+++	
22	Unknown	13.071	++	++	
23	Unknown	13.284		+	
24	Humulene	13.478	++	++	
25	Aromandendrene	13.885	+		
26	Epizonarene	13.866	++		
27	Eicosane	13.971		+	
28	β-cadinene	14.062	++		
29	β-Maaliene	14.078	+		
30	Hexadecane	15.827	+		
31	Unknown	16.142		+	
	Number of compounds		**21**	**20**	**3**

Table 1. List of volatiles organic compounds identified from headspace of healthy plants of tomato (Wild, Floradade and Micro-Tom). Average peak area is indicated with symbol (+) as follow: + 1.00 e06, ++ 1.00e07, +++1.00e08 and ++++ 1.00e09.

	VOCs	RT	Wild	Floradade	Micro-Tom
1	α-Pinene	4.561	+		++
2	β-Pinene	5.277			++
3	1,3,5-Cycloheptatriene, 3,7,7-trimethyl-	5.319	+		
4	o-Cymene	5.344		+	
5	(+)-4-Carene	5.625	+++	++	
6	α-terpinolene	5.697	++		
7	γ-Terpinene	5.783	++	+	
8	(+)-2-Carene	5.79	++	+	
9	α-Phellandrene	5.877		++	
10	β-Phellandrene	6.139	+++		
11	α-Thujene	6.177		+++	
12	β-Sabinene	6.413	++	++	
13	δ-elemene	11.584	++	+	
14	Caryophyllene	12.94	+	++	+
15	Tetradecane	13.02			+
16	Humulene	13.537	+	+	
17	Unknown	16.143		+	
18	Unknown	16.158		+	
	Number of compounds		**11**	**12**	**4**

Table 2. List of volatiles organic compounds identified from headspace of infested plants with *Bactericera cokerelli* nymphs (Wild, Floradade and Micro-Tom). Average peak area is indicated with symbol (+) as follow: + 1.00 e06, ++ 1.00e07 and +++1.00e08.
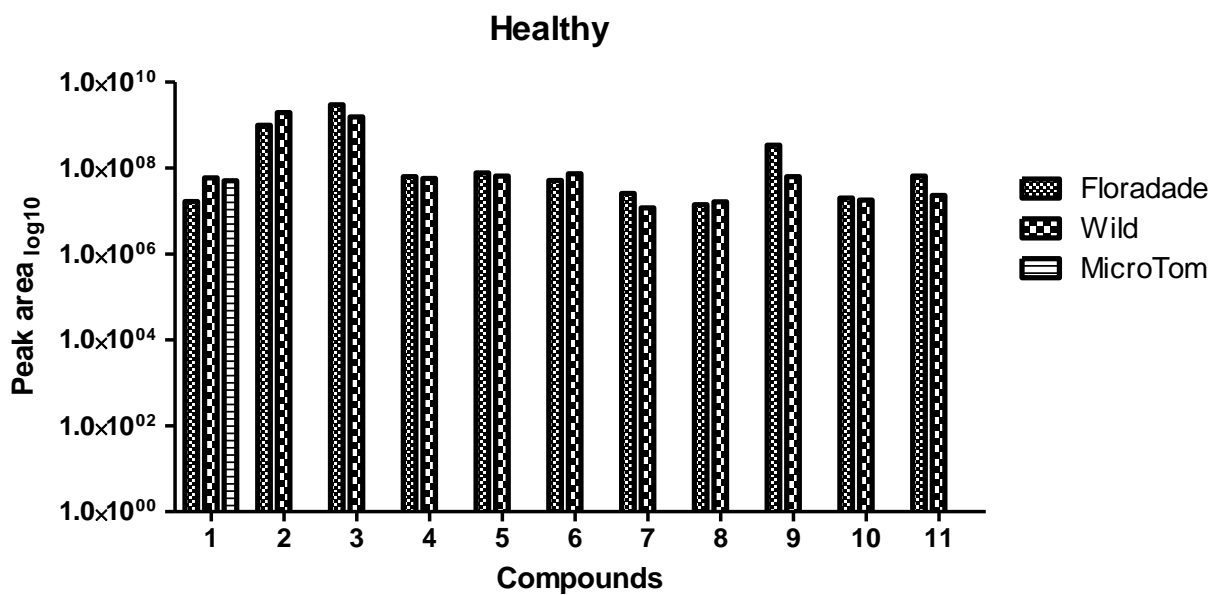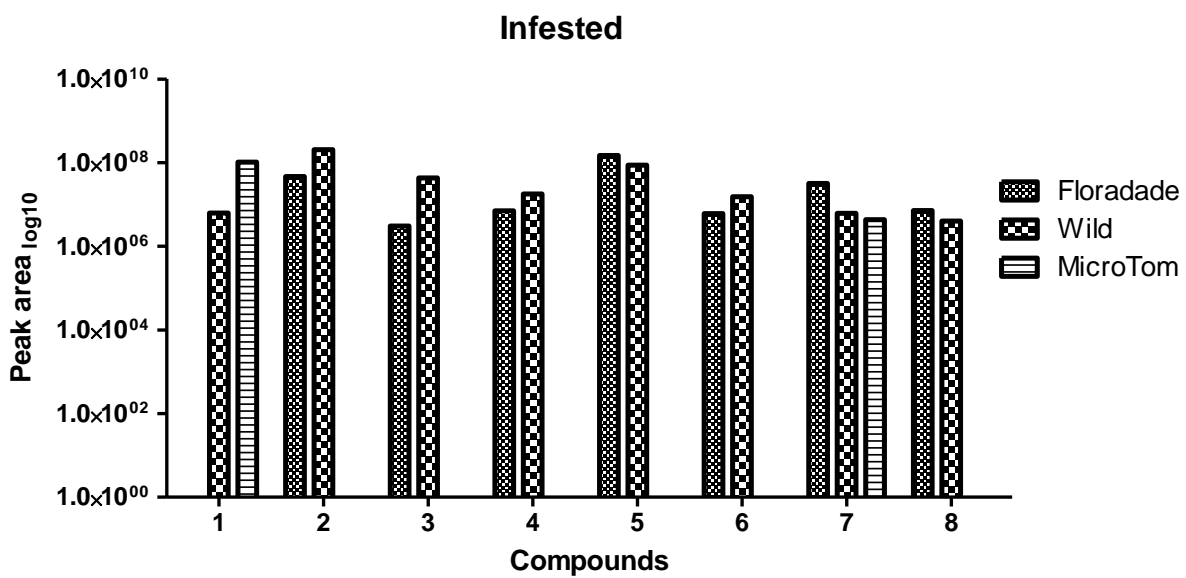
Figures

Healthy

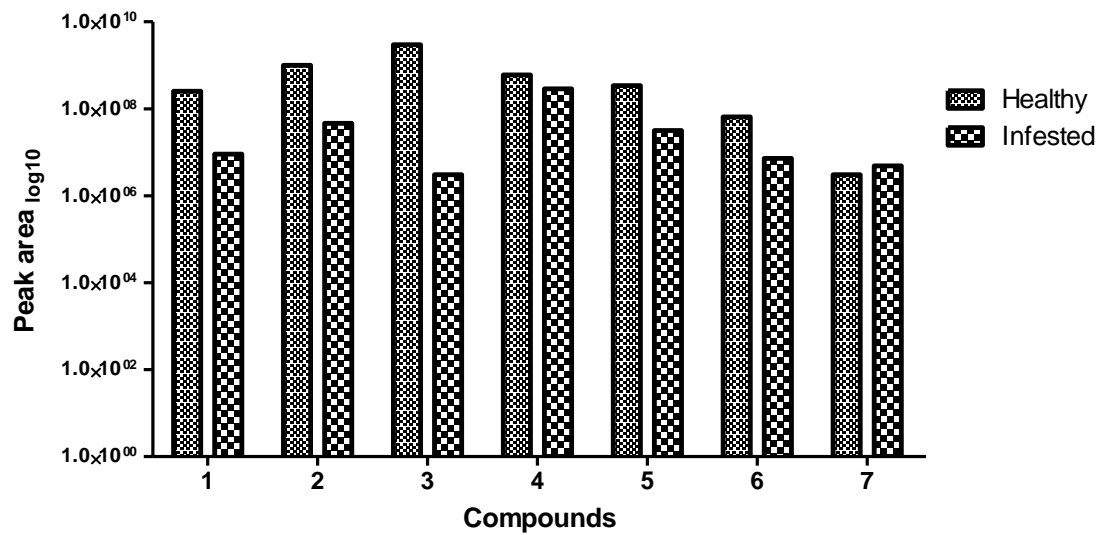Figure 1.

Infested

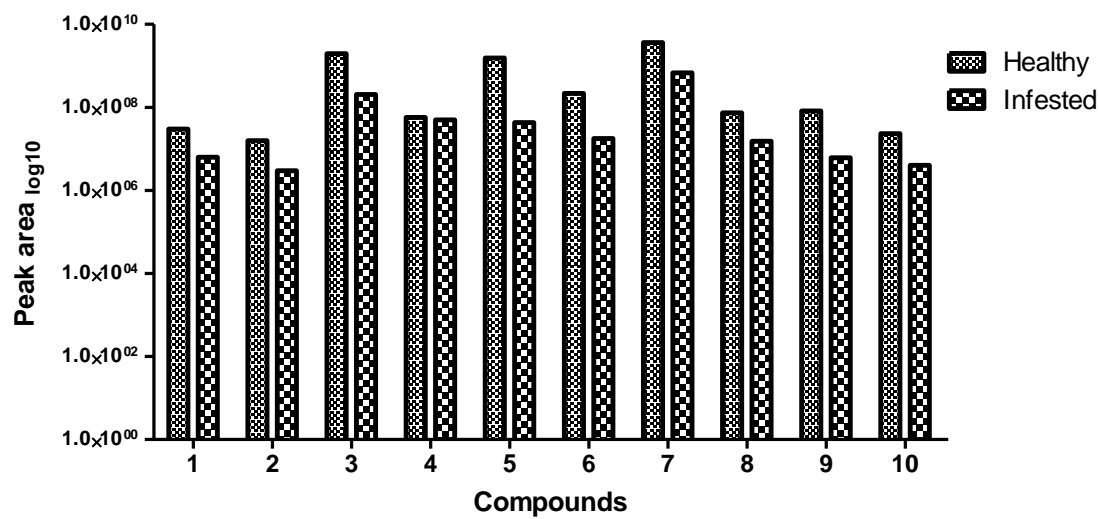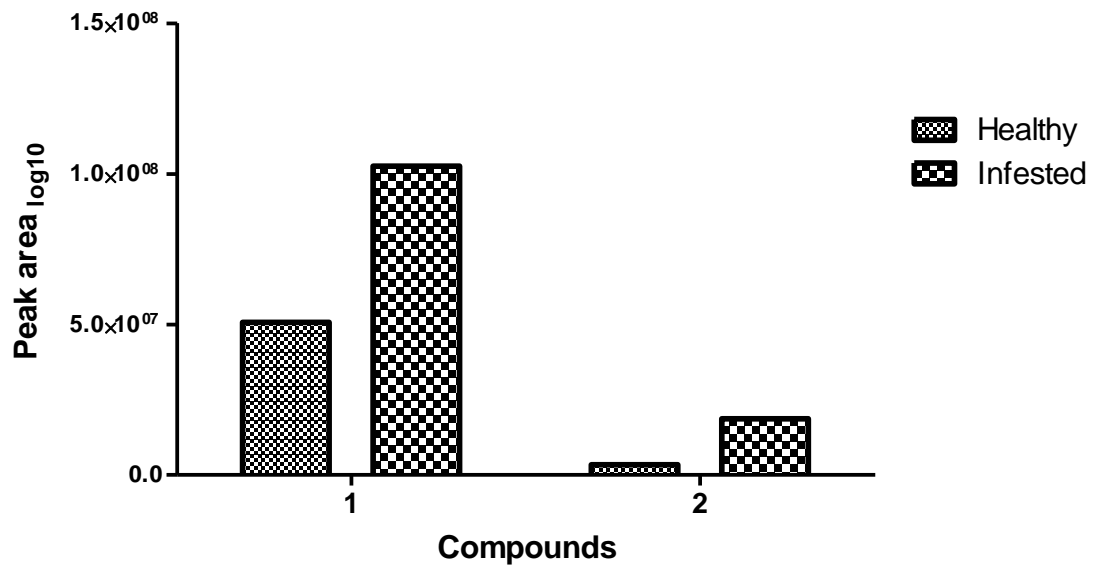Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figures caption

Figure 1. Plant volatiles from healthy plants of three varieties of tomato. Eleven compounds were detected among all varieties and shared in headspace.

Figure 2. Plant volatiles from infested plants of three varieties of tomato. Eight compounds were detected among all varieties and shared in headspace.

Figure 3. Volatile organic compounds detected both healthy and infested *Solanum lycopersicum* cv. Floradade.

Figure 4. Volatile organic compounds detected both healthy and infested *Solanum lycopersicum* cv. Wild.

Figure 5. Volatile organic compounds detected both healthy and infested *Solanum lycopersicum* cv. Micro-Tom.

CONCLUSIONES

- La variedad Floradade es la que presentó un mayor número de oviposición, desarrollo de ninfas y adultos de *B. cockerelli*.

- En las pruebas de preferencia de parasitismo, Floradade fue la que obtuvo un mayor número de ninfas parasitadas, permitiendo que los adultos de *T. triozae* emergieran días antes que en las variedades Silvestre y Micro-Tom.

- En las pruebas de olfatómetro con plantas infestadas y libres de ninfas de *B. cockerelli*, *T. triozae* fue más atraída por las plantas dañadas por ninfas de tercer estadio de *B. cockerelli.*

- Las plantas libres de ninfas de *B.cockerelli* en Floradade y Micro-Tom atrajeron en mayor proporción a adultos de *T. triozae* en la prueba de olfatómetro.

- En el perfil de compuestos volátiles, las variedades Floradade y Silvestre fueron las que más compuestos emitieron en plantas libres e infestadas con ninfas de *B. cockerelli*.

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