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Two volatiles from anthracnose-infected blueberries trigger electrophysiological and aversive behavioral responses in *Drosophila suzukii* (Diptera: Drosophilidae)

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Native to Southeast Asia, the spotted-wing drosophila (*Drosophila suzukii* Matsumura) is an economically important invasive pest of thin-skinned fruits such as raspberries, blueberries, and strawberries worldwide. To reduce the reliance on insecticides for managing this pest, alternative strategies like behavioral manipulation are needed. Previous studies have shown that *D. suzukii* adults avoid blueberry fruits infected with the fungal pathogen *Colletotrichum fioriniae* Marcelino & Gouli, which causes anthracnose fruit rot, leading to the identification of 9 potential repellent compounds. In this study, we further investigated the two most potent of these compounds—ethyl butanoate and ethyl (*E*)-but-2-enoate—to assess their repellent properties on the antennal and behavioral responses of *D. suzukii*. Electroantennogram (EAG) assays revealed that both esters elicited similar dose-dependent responses in male and female *D. suzukii*, which were often stronger than those triggered by 2-pentylfuran, a known repellent of this species. Additionally, we examined the behavioral responses of adult *D. suzukii* to these 3 repellent compounds under semi-field and field conditions using outdoor cages containing potted and planted blueberry bushes, respectively. Results from the cage studies showed that all 3 tested compounds can significantly reduce *D. suzukii* oviposition and adult emergence from blueberry fruits, with ethyl (*E*)-but-2-enoate sometimes outperforming the other compounds. Our findings indicate that the esters ethyl butanoate and ethyl (*E*)-but-2-enoate, which are induced from *C. fioriniae*-infected blueberries, elicit dose-dependent effects on *D. suzukii* antennae and act as effective oviposition deterrents. This supports their potential as promising tools for managing this pest through behavioral strategies.

Keywords: spotted-wing drosophila, invasive pest, volatiles, EAG, oviposition deterrents, semiochemicals

Introduction

The spotted-wing drosophila, *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), is an invasive and highly destructive pest of soft-skinned fruits, including berries, cherries, and grapes (Lee et al. 2011, Walsh et al. 2011, Asplen et al. 2015, Tait et al. 2021). Females of this species have a serrated ovipositor, which allows them to penetrate the skins of ripening and ripe fruits for oviposition (Atallah et al. 2014). Currently, *D. suzukii* is primarily managed through frequent insecticide applications (Diepenbrock et al. 2016, Joshi et al. 2023), which can be costly for growers and may lead to the development of resistance (Gress and Zalom 2019, Disi and Sial 2021, Ganjisaffar et al. 2022, Tabuloc et al. 2024). An alternative method of control that may reduce insecticide use is behavioral manipulation using semiochemicals (Tait et al. 2021). Previous efforts to manage *D. suzukii* with semiochemicals have shown some success (Hampton et al. 2014, Rice et al. 2017, Wallingford et al. 2017,

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2018, Cloonan et al. 2018), demonstrating the potential of this approach. However, discovering new repellent chemicals could further improve this strategy by increasing aversion, enhancing specificity to *D. suzukii*, or identifying more affordable compounds to produce.

Like many insects, *D. suzukii* interacts with microbes in its environment, and these interactions can potentially be exploited to control this pest. Adults of *D. suzukii* are known to be attracted to fermentation odors (Cha et al. 2012, Hamby and Becher 2016) and other microbial volatiles, such as those associated with the symbiotic yeast *Hanseniaspora uvarum* (Niehaus) Shehata, Mrak & Phaff (Hamby et al. 2012, Bueno et al. 2020, Kleman et al. 2022). Many of these fermentation and microbial odors, such as acetic acid, ethanol, methionol, acetoin, isoamyl acetate, and isobutyl acetate, have been used in lure-baited traps for monitoring this pest in the field (Iglesias et al. 2014, Cha et al. 2017, 2018, Swoboda-Bhattarai et al. 2017, Cloonan et al. 2019, Spitaler et al. 2022). However, not all microbial associations elicit positive responses. Pathogenic microbes can provide sources of repellent or oviposition deterrent compounds. For example, 1-octen-3-ol and geosmin, often associated with contamination and spoilage of stored food products, are known repellents against *D. suzukii* (Wallingford et al. 2017). Another microbial volatile, 2-pentylfuran, isolated from fermenting wheat bread dough has also been identified as having oviposition deterrent properties (Cha et al. 2021). Among the 3 previously identified repellents for *D. suzukii*, 2-pentylfuran has shown the most promise due to its effectiveness under field conditions and environmental friendliness. Additionally, Cha et al. (2020) discovered that *D. suzukii* females were less likely to oviposit in raspberries infected with *Botrytis cinerea* Pers., the causative agent of gray mold disease; however, the volatiles responsible for this deterrence remain unidentified. Moreover, *B. cinerea*-infected raspberries significantly reduced larval survival and adult size in *D. suzukii* (Cha et al. 2020). These findings suggest that other plant diseases might similarly influence *D. suzukii* behavior and development.

Blueberries are susceptible to a disease known as anthracnose fruit rot, caused by species of the genus *Colletotrichum*, including *Colletotrichum fioriniae* Marcelino & Gouli (Damm et al. 2012, Pszczółkowska et al. 2016). *Colletotrichum fioriniae* is an ascomycete fungus that spreads to blooms and healthy berries via rain or wind dispersal. Symptoms of anthracnose in blueberries include the development of orange or salmon-colored droplets containing the fungus's conidia and the eventual collapse of the fruit, rendering it unmarketable (Miles and Schilder 2013). Early studies on the interaction between anthracnose and *D. suzukii* have shown that, given a choice, sexually mature females are 3 times more likely to select healthy blueberry fruits over anthracnose-infected ones (Urbaneja-Bernat et al. 2020). Additionally, *D. suzukii* oviposited fewer eggs in infected berries, and anthracnose infection reduced adult emergence. More recent research by Rering et al. (2023) identified 2 esters—ethyl butanoate and ethyl (*E*)-but-2-enoate—from anthracnose-infected blueberries as being equally or more repellent than known *D. suzukii* repellents such as 1-octen-3-ol, geosmin, and 2-pentylfuran. Given these promising results, the present study aims to further investigate whether *D. suzukii* antennae can detect these esters and how these compounds influence the fly's oviposition behavior under semi-field and field cage conditions.

In this study, we evaluated the antennal responses of *D. suzukii* to ethyl butanoate and ethyl (*E*)-but-2-enoate using electroantennography and assessed their oviposition-deterrent activity in outdoor cages. We hypothesized that *D. suzukii* can detect these compounds via their antennae and that they function as oviposition deterrents. These findings could contribute to the development of new compounds for the behavioral manipulation of this pest, offering alternative integrated pest management strategies for *D. suzukii*.

Materials and Methods

Insect Rearing

The *D. suzukii* colony used for experiments was established in 2013 and maintained on a standard artificial diet (Jaramillo et al. 2015) at the Rutgers P.E. Marucci Center (Chatsworth, NJ). The colony was kept under controlled conditions at 22 ± 2 °C, 55 ± 5% relative humidity (RH), and a 16:8 h L:D cycle. To maintain genetic diversity, wild flies were introduced into the colony every 2–3 yr. The flies used in the experiments were 5 to 10 d old, ensuring they were sexually mature (Revadi et al. 2015).

Chemicals

Ethyl butanoate (99%, CAS No. 105-54-4), ethyl (*E*)-but-2-enoate (99%, CAS No. 623-70-1), and 2-pentylfuran (≥ 98%, CAS No. 3777-69-3) were purchased from Sigma-Aldrich (St. Louis, MO, USA).

Electroantennogram Experiments

Electroantennogram (EAG) assays were conducted to determine the antennal response of sexually mature male and female *D. suzukii* to ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentylfuran. The antennal responses of male and female *D. suzukii* to each compound were tested at 5 doses (0.001 mg, 0.01 mg, 0.1 mg, 1 mg, and 10 mg) diluted in n-hexane. The stimulus cartridge preparations, antennal preparations, and EAG apparatus used were similar to those described in Cloonan et al. (2019). Stimulus applicators consisted of a 14.5-cm-long glass Pasteur pipette containing 20 µl of each volatile dose (or n-hexane control) pipetted onto a 6 × 0.5-cm strip of filter paper. The applicators containing the impregnated filter paper were placed under the fume hood for 2 min to allow the n-hexane to evaporate. For the recording and base electrodes, a silver wire was inserted into a drawn capillary tube filled with phosphate-buffered saline (NaCl, 4 g; NA_2HPO_4, 0.57 g; KH_2PO_4, 0.1 g; KCL, 0.1 g in 500 ml distilled water). To attach the base electrode to the fly, the fly's abdomen was removed, and the sharp tip of the saline-filled capillary tube was pulled directly into the thoracic cavity. Once the fly preparation was mounted, the recording electrode was carefully moved toward the antenna using a micromanipulator until the antenna touched the pool of saline solution on the recording electrode. Antennal preparations were exposed to a constant stream of charcoal-filtered and humidified air at a rate of 1.5 L/min.

The EAG apparatus consisted of an IDAC-02 interface board for data acquisition and used Syntech software (Syntech Ltd., Hilversum, The Netherlands) for recording, storing, and quantifying EAG responses. Antennal preparations were primed with 1 mg of acetoin, a known attractant and antennally active compound (Cha et al. 2012, Cloonan et al. 2019), to ensure that the antennae were prepared correctly and responsive (positive control). Then, the antennae were exposed to an n-hexane control, followed by exposure to increasing doses of one of the volatiles. Each antenna was exposed to 4 rounds of each dose of a single compound before being discarded. Six antennae were tested daily: 3 from males and 3 from females. Test and control compounds were applied at 10-s intervals at a pulse rate of 0.5 s, with a 1-min interval between each stimulus. Maximum amplitudes of depolarizations were measured (in millivolts) for each compound with the response from the

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n-hexane-only controls subtracted from the other doses to normalize the antennal response. In total, each dose of each compound was replicated 10 times for each sex.

Semi-field Cage Experiments

Semi-field cage experiments were conducted over a 7-wk period, from 20 June until 9 August of 2023 at the Rutgers P.E. Marucci Research Center (mean ± SE temperature: 23.5 ± 0.27 °C; RH: 78.8 ± 0.9%) to evaluate the oviposition deterrent effects of ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentylfuran against *D. suzukii*. These experiments are considered semi-field because they took place in an isolated open field surrounded by woods with potted plants inside outdoor cages. The cages were constructed using polyvinyl chloride (PVC) pipes (3.8 cm diameter) to construct 1.8 m × 1.8 m × 1.8 m frames. Screen tents (*Lumite* screen portable field cages; BioQuip, CA, USA) were placed over the PVC frames, and large nails were used to secure the tents to the ground (Fig. 1A). Cages were spaced 10 m apart.

To obtain blueberries for the experiment, prior to the start of the experiment, field-grown highbush blueberry (*Vaccinium corymbosum* L. var. "Bluecrop") clusters were bagged early in the season with cloth bags when they were still green to prevent infestation from resident *D. suzukii* populations for use in the experiment. In addition, 80 3–4-yr-old potted blueberry bushes were stripped of their berries and used for the experiment.

On the day of testing, 2 bushes were placed in each cage (Fig. 1B). Each bush in the tent was surrounded by a metal tomato cage. The bagged blueberry fruit clusters in the field were clipped and brought inside the cages. Clusters of 10 berries were created and placed in water picks. Five berry clusters were distributed randomly and evenly on each tomato cage at different heights using green twist ties (Fig. 1B). The sachets used for the treatments were prepared according to the methods described by Gale et al. (2024). They were constructed from 8 cm strips of polyethylene tubing (5.1 cm width, 2 MIL thickness; ULINE, Pleasant Prairie, WI, USA) and polyester felt (Grainger, Lake Forest, IL, USA). One end of the polyethylene tubing was sealed with an impulse sealer. A 5 cm strip of felt was placed inside the sachet's open end, and a 2.5 ml aliquot of each treatment (neat compound) was pipetted onto the felt. The open end was then sealed shut with the impulse sealer, entirely sealing the saturated felt. A hole was punched at the top of each sachet, away from the treatment area to avoid damaging the sealed section, and green twist ties were used to hang the sachets in the center of a bush (Fig 1B). Before loading the sachets, the weights of the empty sachets were taken. The sachets were weighed again directly after loading with the compounds and then a final time after the 24-h test period to measure the emission rates of each volatile.

In each cage, one of the bushes contained a sachet with the test volatile, while the other contained a blank sachet (control). Sachets were hung in the bushes 30 min prior to the start of experiments. Choice tests included (i) control versus control; (ii) control versus ethyl butanoate; (iii) control versus ethyl (*E*)-but-2-enoate; and (iv) control versus 2-pentylfuran. Fifty flies (1:1 male: female) were released in each cage at 18:00 h. After 24 h, the berry clusters were collected and placed in 118 ml plastic cups. Berries were inspected under a dissecting microscope (AmScope SM-1) for the number of eggs laid and were then incubated in 236.6 ml (8-oz) deli containers lined with 2 cotton pads on a laboratory bench at 22 ± 2 °C and

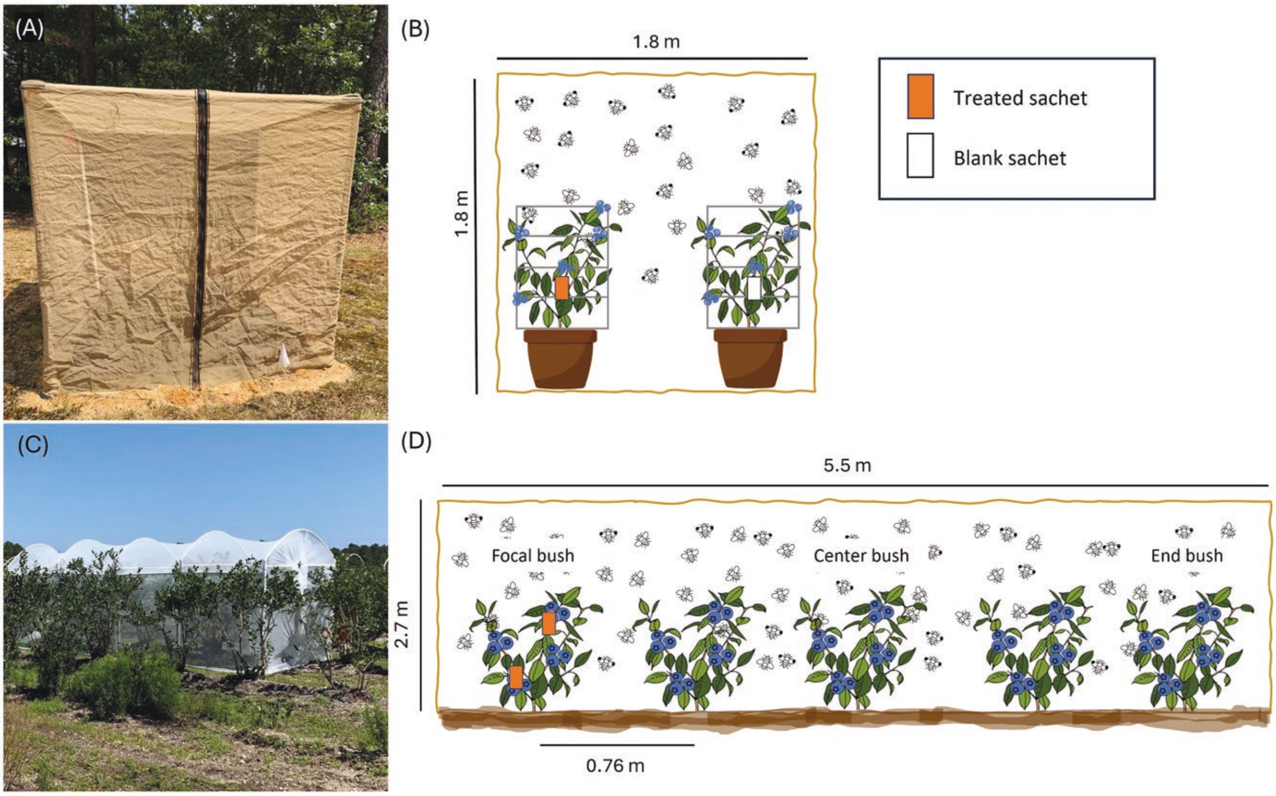

Fig. 1. Cage setups used in semi-field (A and B) and field (C and D) trials. In semi-field trials, each cage consisted of 2 potted blueberry bushes. In field trials, each cage contained 5 cultivated blueberry bushes. One of the bushes (focal bush) within the cage contained a polyethylene sachet with 2.5 ml of the repellent treatments: ethyl butanoate, ethyl (*E*)-but-2-enoate, or 2-pentylfuran (B, D). Control cages did not contain any repellent treatments.

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55 ± 5% relative humidity for 2 wk to monitor for adult emergence. The study was replicated 10 times for each choice combination ($N = 4$ choice combinations × 2 bushes each × 10 replicates = total of 80 bushes; $N = 50$ flies × 4 choice combinations × 10 replicates = total of 2,000 flies).

Field Cage Experiments

Field cage experiments were conducted over 2 separate periods, from 24 to 27 June (mean ± SE temperature: 25.1 ± 0.9 °C; RH: 76.1 ± 5.9%) and 8 to 11 July (27.6 ± 0.1 °C; RH: 80.3 ± 2.1%) of 2024, at the Rutgers P.E. Marucci Research Center using high-bush blueberries (*V. corymbosum* var. "Bluecrop"). The studies were carried out in 5.5 m long × 2.7 m tall cages, constructed with a PVC pipe frame covered with No-See-Um mesh (Quest Outfitters Inc., Sarasota, FL, USA) (Fig. 1C). Cages were placed in separate rows within a blueberry field, with bushes spaced approximately 0.76 m apart within the rows and 3.05 m between rows. Each row contained 2 cages at least 9 m in distance. To avoid interference between treatments, alternate cages were used during testing, ensuring that no adjacent cages contained sachets simultaneously.

Two, 3-m rebar poles were used to reinforce the mesh on the long sides of each cage as well as 10 cm long garden staples to hold the mesh flush to the ground, while the shorter ends were secured with clips to allow access to the cage. Each cage contained 5 blueberry bushes approximately 1.5 m in height. Sachets containing ethyl butanoate, ethyl (*E*)-but-2-enoate, or 2-pentylfuran were prepared as described before. To test the effects of the repellents on the treated (focal) bush and in neighboring bushes at various distances, 2 sachets of the same compound were hung from one of the end bushes in each cage (Fig. 1D). There were 4 treatments: (i) ethyl butanoate, (ii) ethyl (*E*)-but-2-enoate, (iii) 2-pentylfuran, and (iv) control (no repellent). Each treatment was replicated 4 times, with each cage assigned to a single treatment, resulting in a total of 16 cages.

Twenty-four hours after deploying the sachets, 120 flies (approximately 60 males and 60 females) were released into each cage at 18:00 h ($N = 120$ flies × 4 treatments × 4 replicates = 1,920 total flies). To ensure even distribution within the cages, 30 flies were released at 4 equidistant points between the bushes. A pre-sampling of the berries, conducted before the flies were released, confirmed the absence of any infestation. Berries were then collected 1-, 2-, and 3-d post-treatment. From every other bush (starting at the focal bush) in the cage, 50 berries from the top half and 50 from the bottom half were collected into 2 separate 236.6 ml deli containers lined with 2 cotton pads. From each berry sample, a random subsample of 10 berries were examined and egg counts recorded before being returned to the original container. The blueberries were incubated on a light bench in the laboratory for up to 2 wk, as previously described, and adult emergence was recorded. The sachets were weighed before deployment and 3 d after deployment to measure the emission rates of each compound.

Statistical Analysis

To analyze the effect of dose of the 3 repellents on *D. suzukii* antennal responses, a generalized linear model (GLM) was used with a Poisson distribution and a log link function in SPSS Statistics 23.0 (IBM Corp, Armonk, NY, USA). The model included "Treatment" (ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentylfuran), "Dose," "Sex," and their interactions as independent variables. This analysis, when significant, was followed by post hoc Bonferroni tests ($\alpha = 0.05$) to determine individual differences among groups. Prior to analysis, EAG data were normalized relative to the response to the n-hexane control.

Semi-field cage data were analyzed using paired *t*-tests to determine differences between the number of eggs laid and adults that emerged from treated berries compared to control berries, and survival data were analyzed using 2-way analysis of variance (ANOVA) (R statistical software version 4.1.1; R Development Core Team, Vienna, Austria). In addition, a deterrence index (DI) was calculated for each treatment as follows:

$$DI = \frac{(n_{control} - n_{volatile})}{n_{total}}$$

Where n_{control}, n_{volatile}, and n_{total} are the number of eggs laid in the control fruits, repellent treatment fruits, and total number of eggs laid in the control and repellent treatment fruits, respectively. The DI values were compared among treatments using ANOVA (R statistical software). Before the analysis, data were checked for normality and equal variance using an Anderson–Darling test and Levene's test, respectively.

Field cage data for both oviposition and adult emergence were non-normal, so non-parametric tests were applied using R statistical software. The effects of "Treatment" (untreated control, ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentylfuran) across "Bush Position" (focal, center, end) and "Day After Treatment" (1, 2, 3 DAT) were assessed using the Kruskal–Wallis Test. When significant Treatment effects were found, post-hoc separation was performed using Dunn's Test. Initial analyses showed no significant differences in oviposition or adult emergence based on location on the bush (top vs. bottom); therefore, the data were averaged and analyzed at the bush level.

Finally, the emission rates of compounds in the semi-field and field cage studies were calculated by subtracting the final weight of the sachets from the initial weight and dividing by the time interval (24 h or 3 d). These rates were then compared across repellent treatments using ANOVA, with Tukey pairwise comparisons conducted when significant differences were found.

Results

Electroantennogram Experiments

Both male and female *D. suzukii* exhibited dose-dependent antennal responses to ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentylfuran (Table 1; Fig. 2). The strength of the EAG responses varied among treatments, with ethyl butanoate and ethyl (*E*)-but-2-enoate eliciting stronger antennal responses than 2-pentylfuran (Table 1; Fig. 2). There was no significant effect of sex on the antennal responses to these compounds, nor was there a significant

Table 1. Results of a generalized linear model (GLM) for the effects of "Treatment" (ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentylfuran), "Dose," "Sex," and their interactions on the electroantennogram (EAG) responses of *Drosophila suzukii*.

Source of Variation	Wald χ^2	df	*P*[a]
(Intercept)	1578.21	1	**<0.001**
Treatment	91.72	2	**<0.001**
Dose	477.87	4	**<0.001**
Sex	0.05	1	0.817
Treatment × Dose	67.78	8	**<0.001**
Treatment × Sex	5.21	2	0.074
Dose × Sex	1.89	4	0.754
Treatment × Dose × Sex	1.16	8	0.997

[a] Significant *P* values are indicated in bold.

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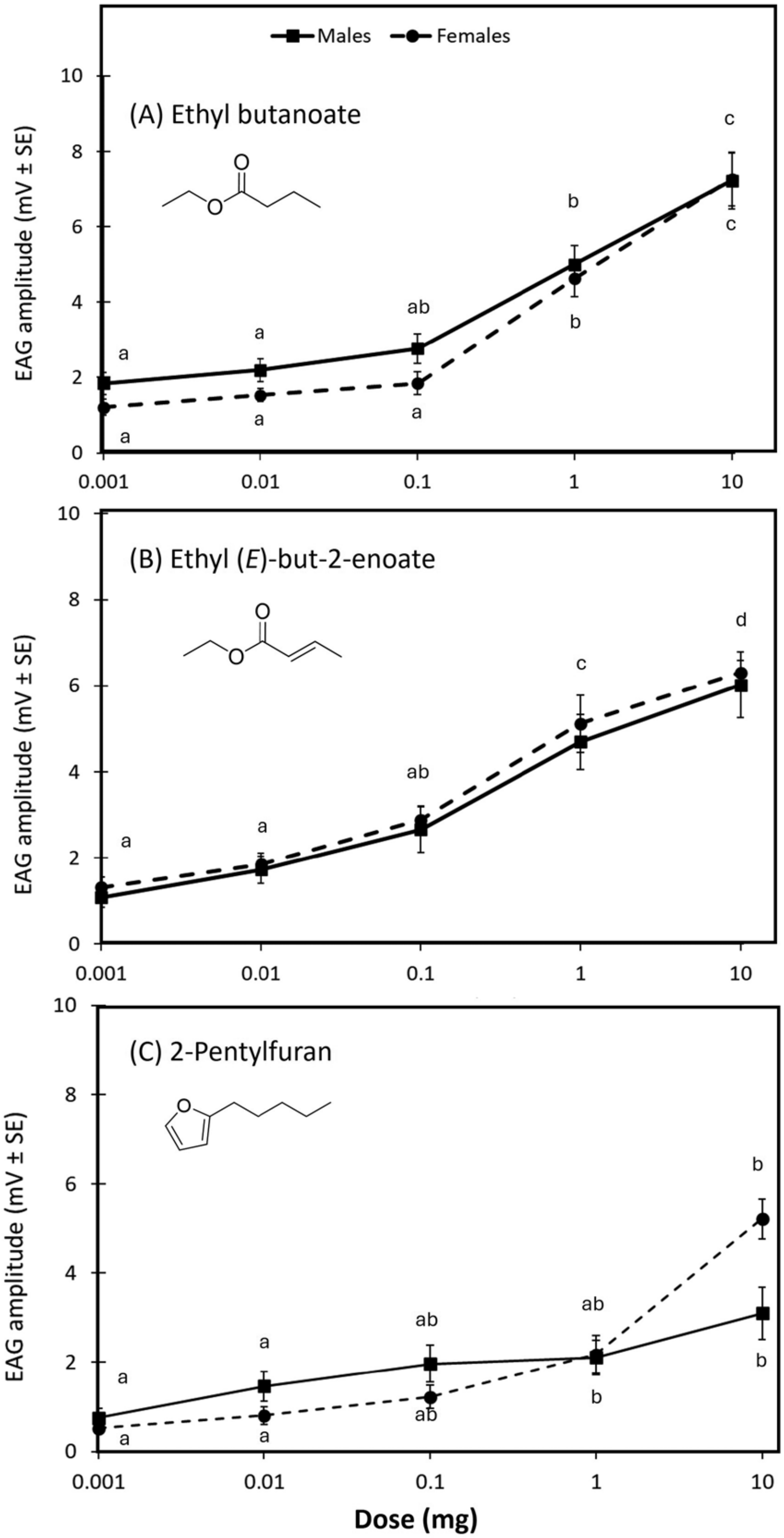

Fig. 2. Electroantennogram (EAG) response curves of male (solid lines) and female (dashed lines) *Drosophila suzukii* antennae to ethyl butanoate (A), ethyl (*E*)-but-2-enoate (B), and 2-pentylfuran (C). EAG amplitudes are presented as antennal depolarizations (mV ± SE) normalized relative to the response to the n-hexane control. Different letters indicate significant differences among doses. *N* = 10.

interaction between treatment and sex (Table 1), indicating that the antennal responses of male and female *D. suzukii* to ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentylfuran were similar. Although the EAG responses increased with rising doses of the compounds, the antennae of *D. suzukii* responded more strongly to ethyl butanoate and ethyl (*E*)-but-2-enoate than to 2-pentylfuran at higher doses (Fig. 2), as indicated by the significant treatment-by-dose interaction (Table 1).

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Semi-field Cage Experiments

Semi-field cage assays using potted blueberry plants were used to test the efficacy of ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentylfuran on *D. suzukii* oviposition. There were no differences in the emission rates of the 3 compounds ($F = 1.66$; df = 2,12; $P = 0.231$; mean emission rates (± SE) were 70.4 ± 14.2 mg/h for ethyl butanoate, 54.9 ± 8.9 mg/h for ethyl (*E*)-but-2-enoate, and 82.3 ± 7.6 mg/h for 2-pentylfuran). *Drosophila suzukii* consistently laid fewer eggs in berries paired with the repellent treatments in comparison to control berries (Fig. 3A). Flies laid 54% fewer eggs

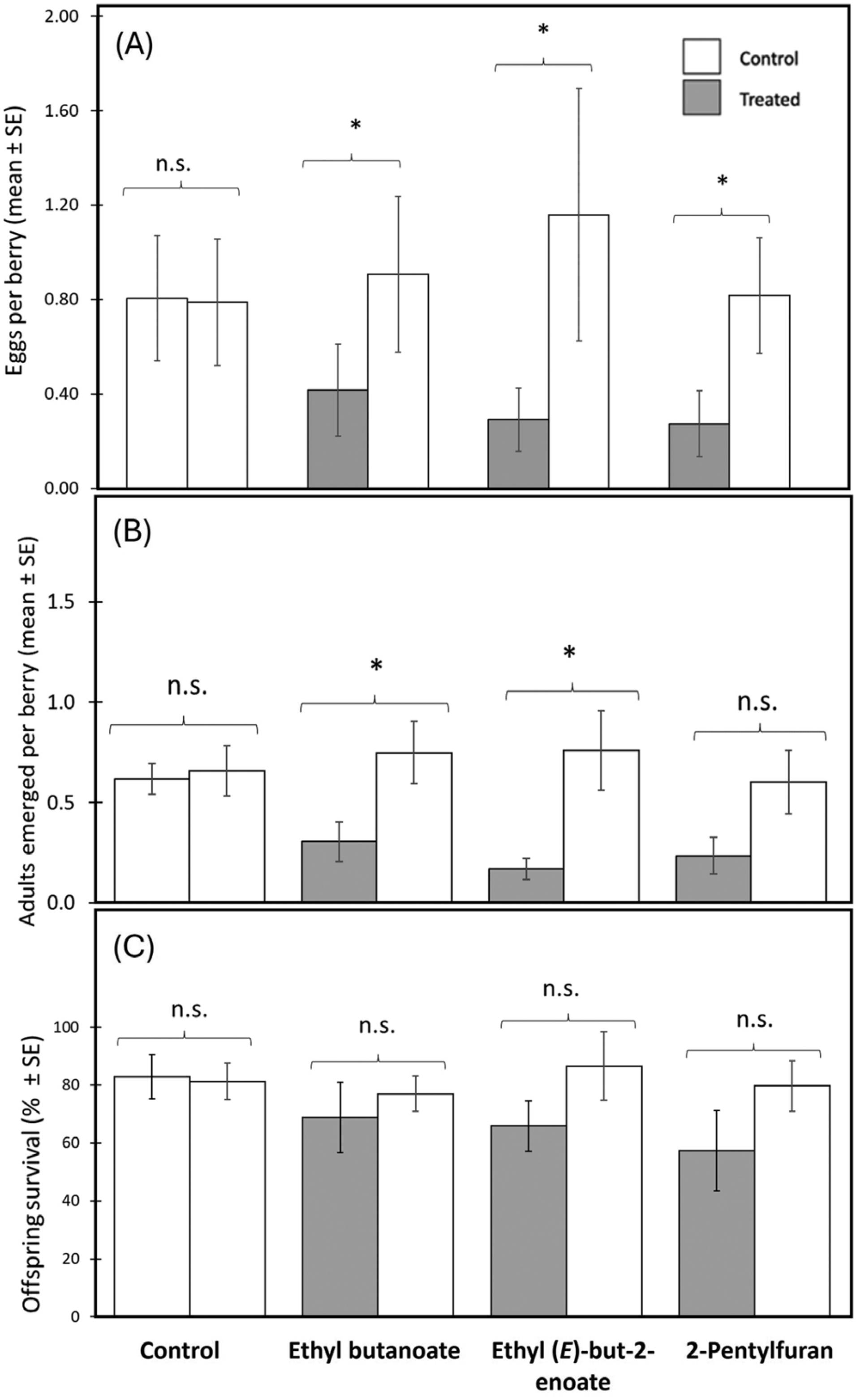

Fig. 3. Effects of ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentyfuran on *Drosophila suzukii* oviposition (A), adult emergence (B), and survival from eggs to adults (C) in semi-field cage studies. An asterisk indicates significant differences between the control (white bars) and the treated (gray bars) berries within each cage. n.s. = no significant differences between the control and treatment. $N = 10$.

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in ethyl butanoate-treated berries ($t = 2.29$, $P = 0.047$), 75% fewer berries in ethyl (*E*)-but-2-enoate treated berries ($t = 3.76$, $P = 0.005$), and 67% fewer eggs in 2-pentylfuran treated berries (Fig. 3A).

When comparing the emergence of adult progeny (Fig. 3B), more flies emerged from the control berries compared to the berries treated with the 2 anthracnose-associated compounds, with 59% fewer flies emerging from ethyl butanoate treated berries ($t = 4.07$, $P = 0.003$) and 78% fewer flies emerging from ethyl (*E*)-but-2-enoate treated berries ($t = 2.81$, $P = 0.02$). The difference in adult emergence between untreated berries and 2-pentylfuran treated berries was nonsignificant ($t = 2.06$, $P = 0.069$).

The percentage of eggs that survived to adulthood ranged from 57% (± 14%) to 83% (± 8%) across all treatments (Fig. 3C). A 2-way ANOVA showed no significant differences in offspring survival among the treatments or between treatments and controls (all P values > 0.05), indicating that the treatments only affected *D. suzukii* oviposition behavior which resulted in reduced adult emergence.

After calculating the DI based on the number of eggs laid within each cage, ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentylfuran all performed similarly and were significantly different from the control ($F = 4.85$; df = 4,36; $P = 0.005$) (Fig. 4).

Field Cage Experiments

Field cage assays using cultivated blueberry bushes tested the efficacy of ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentylfuran on *D. suzukii* oviposition. In these trials, the emission rates differed significantly among the 3 tested compounds ($F = 16.29$; df = 2,27; $P < 0.001$). The emission rates for ethyl butanoate (mean ± SE = 697.97 ± 7.96 mg/day) and ethyl (*E*)-but-2-enoate (679.23 ± 17.73 mg/day) were significantly higher than those for 2-pentylfuran (559.73 ± 23.54 mg/day).

Egg counts were higher in the control than all the repellent treatment groups regardless of bush position or DAT (Fig. 5A). Among the 3 repellent treatments, the response varied depending on the bush position and DAT. At 1 DAT, all repellent treatments reduced egg counts in the focal bush compared to the control ($\chi^2 = 222.01$; df = 3; $P < 0.001$), but there were no differences among them; 2-pentylfuran was lower at the central bush ($\chi^2 = 206.70$; df = 3, $P < 0.001$); and 2-pentylfuran and ethyl (*E*)-but-2-enoate had the fewest eggs at the end bush ($\chi^2 = 143.43$, df = 3, $P < 0.001$) (Fig. 5A). At 2 DAT, the treatments again demonstrated similar oviposition repellency at the focal bush ($\chi^2 = 174.37$; df = 3; $P < 0.001$), but ethyl (*E*)-but-2-enoate had the lowest egg counts at both the center ($\chi^2 = 151.81$; df = 3; $P < 0.001$) and the end bush ($\chi^2 = 148.01$; df = 3; $P < 0.001$) (Fig. 5A). By 3 DAT, ethyl (*E*)-but-2-enoate had the lowest egg count at all 3 bushes sampled (focal: $\chi^2 = 91.26$; df = 3; $P < 0.001$; center: $\chi^2 = 91.31$; df = 3; $P < 0.001$; end: $\chi^2 = 85.12$; df = 3; $P < 0.001$) (Fig. 5A).

The emergence of adult progeny was also higher in the untreated control cages than any of the repellent treatments (Fig. 5B). At 1 DAT and 2 DAT, there were differences in adult emergence between the control and all the repellent treatments at the focal bush (1 DAT: $\chi^2 = 25.01$; df = 3; $P < 0.001$; 2 DAT: $\chi^2 = 25.48$; df = 3; $P < 0.001$) but no differences among them; ethyl (*E*)-but-2-enoate had the fewest adults emerge at the center (1 DAT: $\chi^2 = 25.48$; df = 3; $P < 0.001$; 2 DAT: $\chi^2 = 23.20$; df = 3; $P < 0.001$) and end bush (1 DAT: $\chi^2 = 19.56$; df = 3; $P < 0.001$; 2 DAT: $\chi^2 = 14.94$; df = 3; $P < 0.001$) (Fig. 5B). At 3 DAT, 2-pentylfuran and ethyl (*E*)-but-2-enoate had the lowest adult emergence at the focal ($\chi^2 = 19.20$; df = 3; $P < 0.001$) and center bush ($\chi^2 = 15.72$; df = 3; $P < 0.001$) but, at the end bush, only ethyl (*E*)-but-2-enoate was significantly different compared to the other repellents ($\chi^2 = 15.35$; df = 3; $P < 0.001$) (Fig. 5B).

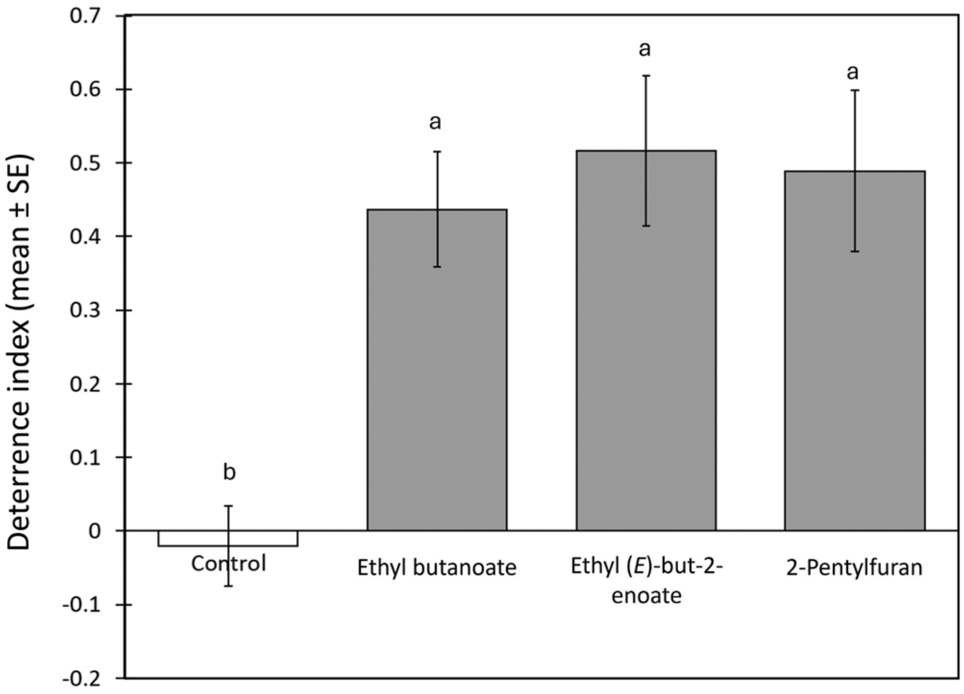

Fig. 4. Effects of ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentyfuran on the deterrence index of *Drosophila suzukii* in semi-field cage studies. The deterrence index was calculated as (number of eggs per berry in the control—number of eggs per berry in the treatment)/total number of eggs per berry. Different letters indicate significant differences among treatments. *N* = 10.

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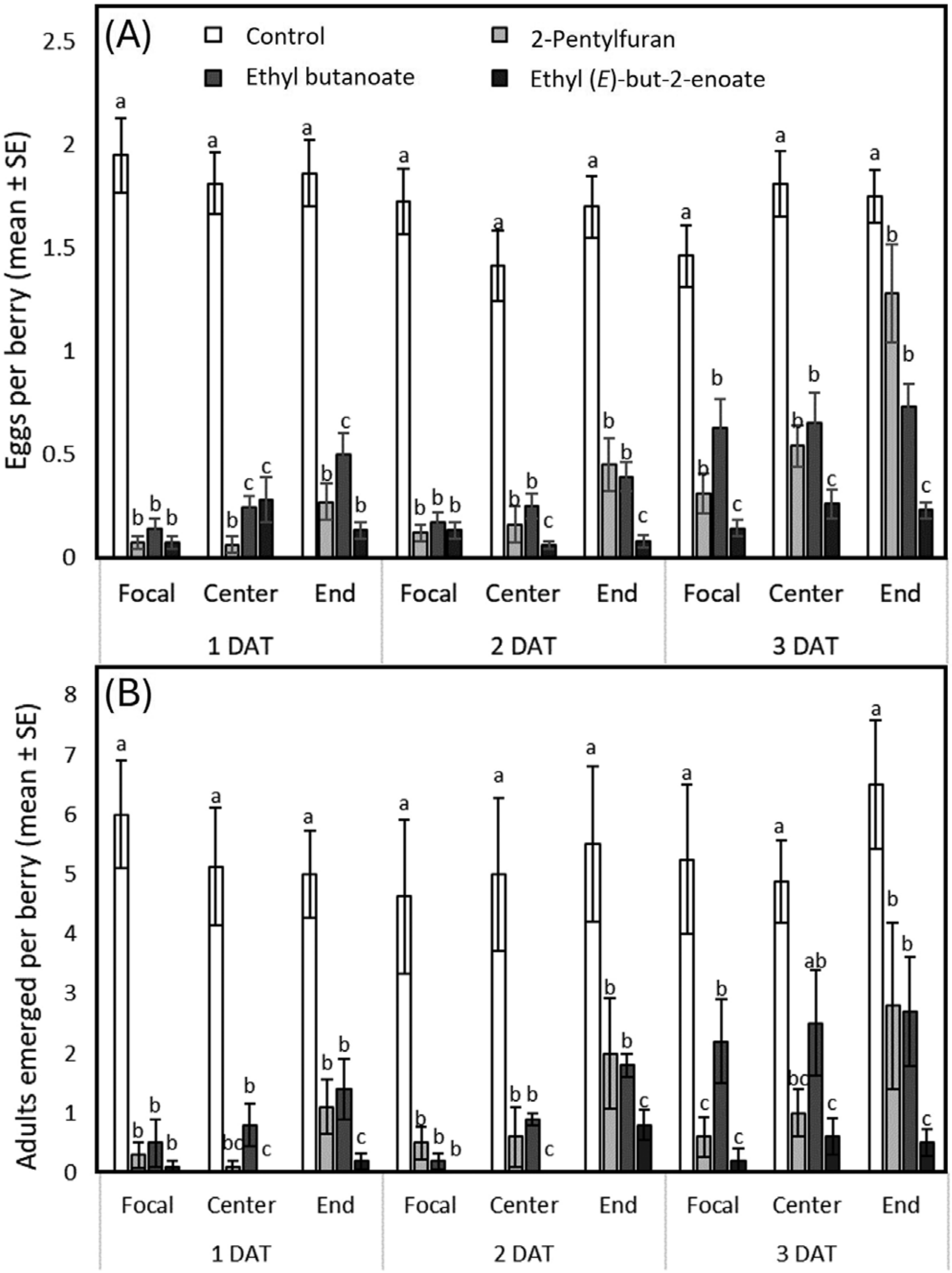

Fig. 5. Effects of an untreated control, ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentyfuran on oviposition (A) and adult emergence (B) of *Drosophila suzukii* in field cages. Egg counts represent the mean number of eggs from a 10-berry subsample, while adult emergence refers to the average number of *D. suzukii* adults emerging from a 50-berry sample. *N* = 4.

Discussion

This study demonstrated that (i) both male and female antennae of *D. suzukii* can detect ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentylfuran in a dose-dependent manner; and (ii) these repellent compounds reduce *D. suzukii* oviposition and adult emergence in blueberry fruits under semi-field and field cage conditions.

After anthracnose-infected blueberries were found to repel *D. suzukii* (Urbaneja-Bernat et al. 2020), Rering et al. (2023) screened 14 volatiles emitted at higher levels in infected berries compared to healthy ones for their repellent activity against this pest in laboratory studies. They found that 9 of these volatiles had repellent properties. Among them, 2 esters—ethyl butanoate and ethyl (*E*)-but-2-enoate—showed the strongest repellent effects, and as demonstrated in this study, these compounds also trigger strong dose-dependent antennal responses in adult *D. suzukii* and act as oviposition deterrents under semi-field and field cage conditions. These compounds are naturally present in the headspace of blueberries and are mainly associated with fruit ripening (Beaulieu et al. 2014, Farneti et al. 2017). Since anthracnose infections cause rapid ripening and collapse of the fruit (Miles and Schilder 2013), simultaneously the emission rate of these volatiles increases (Rering et al. 2023). Given that *D. suzukii* are typically attracted to ripening or ripe fruits for oviposition rather than overripe ones (Lee et al. 2011, Keesey et al. 2015), the observed oviposition deterrent effects in this study may indicate that the flies perceive the fruits as beginning to rot, thus discouraging them from laying eggs.

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Ethyl butanoate has been previously identified as an antennally active compound in *D. suzukii* (Cloonan et al. 2019, Urbaneja-Bernat et al. 2021) and shown to reduce attraction to lures (Cha et al. 2012). However, its role as an oviposition deterrent under field conditions had not been confirmed until this study. Ethyl (*E*)-but-2-enoate, while structurally similar to ethyl butanoate, has also not been previously identified as an oviposition deterrent. Both compounds elicited similar dose-dependent responses in EAG assays for both male and female *D. suzukii*. However, when compared to the known repellent 2-pentylfuran, these esters showed comparable or stronger antennal detection efficacy, especially at higher doses. A similar trend was observed in the semi-field cage studies, where ethyl butanoate, ethyl (*E*)-but-2-enoate, and 2-pentylfuran significantly reduced *D. suzukii* oviposition in treated berries compared to the control. In the field cage studies, ethyl (*E*)-but-2-enoate tended to outperform both ethyl butanoate and 2-pentylfuran, particularly at longer distances from the focal plant and after at least 3 d of deployment, demonstrating greater oviposition deterrent activity.

Urbaneja-Bernat et al. (2020) demonstrated that only female *D. suzukii* were repelled or deterred from ovipositing by volatiles from anthracnose-infected fruits, likely because they are searching for suitable oviposition sites. Anthracnose infection likely reduces the quality of fruits for *D. suzukii* offspring development (Urbaneja-Bernat et al. 2020), showing a positive relationship between female oviposition preference and offspring performance. However, when examining the antennal response of *D. suzukii* to ethyl butanoate and ethyl (*E*)-but-2-enoate, both males and females showed similar responses, indicating that both sexes can detect these compounds. Although males may be less behaviorally responsive to anthracnose-infected fruits than females, both male and female *D. suzukii* were found to be repelled by these compounds in laboratory assays (Rering et al. 2023). The role of these volatiles in influencing male behaviors remains unclear.

Ethyl butanoate and ethyl (*E*)-but-2-enoate have demonstrated equal or superior performance compared to other known *D. suzukii* repellents, such as 2-pentylfuran, geosmin, and 1-octen-3-ol (Rering et al. 2023; this study), showing promise as effective repellents and oviposition deterrents against this pest. Future research should explore whether ethyl butanoate and ethyl (*E*)-but-2-enoate synergize with other *D. suzukii* repellents or with repellent compounds identified in anthracnose-infected blueberries (Rering et al. 2023). Combining these compounds could help maintain their repellent efficacy in the field, especially since ethyl butanoate and ethyl (*E*)-but-2-enoate are more volatile than other known *D. suzukii* repellents. Further research is also needed to identify optimal deployment methods for these compounds. In the field cage study, ethyl butanoate and ethyl (*E*)-but-2-enoate exhibited higher emission rates than 2-pentylfuran, with minimal amounts remaining in the sachets after 3 d. Employing slow-release technologies, such as the inert matrix SPLAT (Specialized Pheromone and Lure Application Technology) (Wallingford et al. 2016a), aerosol diffusers (Stockton et al. 2021), and nanoencapsulation (de Oliveira et al. 2018), could help sustain adequate emission rates of these compounds in the field.

Previously, repellents against *D. suzukii* have shown some success in reducing infestations in raspberries in both greenhouse and field studies (Wallingford et al. 2016a, 2016b, Stockton et al. 2021). However, repellents alone are typically insufficient to fully eradicate *D. suzukii* infestations, which is critical in crops like blueberries where there is zero tolerance for infested fruit (Rodriguez-Saona et al. 2019). Nonetheless, repellent or oviposition deterrent compounds can be valuable tools when used in combination with other behavioral manipulation methods. For example, they could be paired with attract-and-kill devices to develop push-pull systems for *D. suzukii*. Push-pull systems work by using a repellent or oviposition deterrent to "push" the pest away from the target crop, while the "pull" component attracts pests to a kill device (Cook et al. 2007). Push-pull systems using 1-octen-3-ol (Wallingford et al. 2018) or methyl benzoate (Gale et al. 2024) as the push component, combined with an attract-and-kill device as the pull component, have already shown some success in managing *D. suzukii* in raspberries and blueberries.

In conclusion, the current study provides additional evidence that the esters ethyl butanoate and ethyl (*E*)-but-2-enoate, derived from pathogen-infected fruit, could serve as promising oviposition deterrents for *D. suzukii*. While previous studies have shown that pathogen infections and isolated compounds can repel *D. suzukii* and deter oviposition (Urbaneja-Bernat et al. 2020, Cha et al. 2021, Rering et al. 2023), the physiological and behavioral effects of specific compounds remained largely unexplored. In this study, ethyl butanoate and ethyl (*E*)-but-2-enoate elicited dose-dependent antennal responses in *D. suzukii* and significantly reduced oviposition and adult emergence in semi-field and field cage trials, performing comparably to, or sometimes even better than, the known *D. suzukii* repellent, 2-pentylfuran. Further research is necessary to evaluate the spatial and temporal efficacy of these compounds, as well as optimal deployment methods, under more realistic field conditions with natural levels of pest pressure. Additionally, their repellent effects on other pests, as well as their compatibility with other *D. suzukii* management tactics such as biological control, need to be explored. Nevertheless, the strong antennal responses and oviposition deterrent effects observed suggest that these compounds could serve as valuable tools for managing *D. suzukii* behavior in the field.

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Author contributions

Amanda Quadrel (Conceptualization [Equal], Data curation [Equal], Formal analysis [Equal], Methodology [Equal], Writing—original draft [Equal], Writing—review & editing [Equal]), Beth Ferguson (Data curation [Equal], Formal analysis [Equal], Methodology [Equal], Writing—review & editing [Equal]), Caitlin Rering (Conceptualization [Equal], Investigation [Equal], Methodology [Equal], Writing—review & editing [Equal]), Pablo Urbaneja Bernat (Conceptualization [Equal], Investigation [Equal], Writing—review & editing [Equal]), and Cesar Rodriguez-Saona (Conceptualization [Equal], Investigation [Equal], Methodology [Equal], Resources [Equal], Supervision [Equal], Writing—original draft [Equal], Writing—review & editing [Equal])

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Conflicts of interest. None declared.

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