Research Article

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Methyl *N,N*-dimethylanthranilate and ethyl propionate: repellents effective against spotted wing drosophila, *Drosophila suzukii*

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Abstract

BACKGROUND: Spotted wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), is an economically important pest of soft and stone fruit crops. The aim of this study was to identify repellents, formulated in dispensers, which could protect crops from *D. suzukii*. Fourteen potential repellents were screened against summer- and winter-morph *D. suzukii* through electroantennography and behavioural bioassays. Repellents effective in the laboratory were tested in polytunnels to determine their efficacy in reducing catches in fruit-baited traps. Further trials of three potential repellents were conducted to determine the distances over which repellent dispensers could reduce *D. suzukii* emergence in a strawberry crop.

RESULTS: All 14 chemicals screened were detected by the antennae of both *D. suzukii* morphs. Hexyl acetate and geosmin both elicited a significantly greater corrected EAG response in summer morphs than winter morphs. Summer-morph *D. suzukii* were repelled by butyl acetate, ethyl propionate, methyl *N,N*-dimethyl anthranilate, geosmin, methyl salicylate, DEET and benzaldehyde at one or more doses test in laboratory bioassays. Winter morphs were repelled by ethyl propionate, methyl anthranilate, methyl *N,N*-dimethyl anthranilate, DEET, benzaldehyde and butyl anthranilate at one or more of the doses tested in the laboratory. Ethyl propionate, methyl *N,N*-dimethylanthranilate and benzaldehyde repelled both morphs from fruit-baited traps in polytunnel trapping trials. Ethyl propionate and methyl *N,N*-dimethylanthranilate reduced emergence of *D. suzukii* in a strawberry crop over 3–5 m.

CONCLUSIONS: Ethyl propionate and methyl *N,N*-dimethylanthranilate may protect strawberry crops against *D. suzukii*. Future work should test these repellents in combination with attractants in a 'push-pull' strategy.

Supporting information may be found in the online version of this article.

Keywords: horticulture; integrated pest management; repellents; semiochemicals; spotted wing drosophila

1 INTRODUCTION

Spotted wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), is a major insect pest of soft and stone fruit crops.[1] First reported from South-east Asia, *D. suzukii* is now established in the US,[2] mainland Europe[3] and was first reported in the UK in 2012.[4] Female *D. suzukii* possess a serrated ovipositor with which they can lay eggs in ripening fruit resulting in unmarketable produce.[1] Subsequent economic losses resulting from reduced revenue from sale of fruit are compounded by additional costs associated with prevention and control of *D. suzukii*.[5] Control measures include use of exclusion netting,[5,6] which may require additional infrastructure with associated costs,[5,7] and labour-intensive sanitation to remove and destroy infested fruit.[8,9] Odour-baited traps[10,11] are used for monitoring[10,12] and to time use of insecticide sprays where permitted. Use of synthetic pesticides is restricted in many territories and growers must comply with residue limits and pre-harvest intervals for treated fruit.[8] Pesticide use also may promote the onset of resistance in *D. suzukii* populations and interfere with integrated pest management strategies against other pests utilizing beneficial insects.[8,12] Attractants may be applied to reduce populations through mass trapping or attract and kill strategies, but risk increasing the number of *D. suzukii* moving into crops.[13]

Repellents, which could prevent *D. suzukii* from laying eggs in fresh fruit, could be a viable tool for use in integrated pest management. While repellents are widely used to protect people and animals from ticks and biting insects,[14–16] similar technologies have been underutilized for plant protection,[17] perhaps as a consequence of perceived difficulties in maintaining effective concentrations in the field.[13] Repellents designed for human

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use often are applied topically or close to the skin on clothing to reduce insect landing and biting.[18] A similar strategy may be undesirable in agriculture and horticulture if repellents applied directly to plants leave toxic residues or taint food crops. However, recent work has demonstrated that a synthetic repellent released from sachet dispensers can be used in combination with attractive sex pheromones to reduce damage to strawberries from the mirid bug *Lygus rugulipennis*.[19] A similar 'push–pull' strategy,[20] where repellents are used to dissuade insects ovipositing in crops while being lured into traps with semiochemical attractants, may provide a new tool for protecting crops from *D. suzukii*.[13]

There are no commercially available repellents for use against *D. suzukii*. Despite numerous successful laboratory studies, field or semi-field trials have generally been less successful.[13,21–27] Ideally, repellent formulations should be effective against both summer- and winter-morph *D. suzukii*. The two morphs inhabit different environments[28] and exhibit distinct behaviours, with females undergoing reproductive diapause during winter.[29] Previous work has shown that the two morphs differ in their olfactory and behavioural responses to semiochemicals[30] although they can both be caught using fermentation-based traps.[31] The two morphs are both important targets for control as summer-morph females oviposit in fruit, and the cold-tolerant winter morph overwinters in woodlands before moving into crops in early spring.[12,32,33]

The aim of this study was to determine whether repellents, formulated in suitable controlled-release dispensers, could reduce damage to strawberries caused by *D. suzukii* under semi-field conditions. Fourteen potential *D. suzukii* repellents for testing were selected from the literature and research undertaken at NRI and NIAB East Malling. We first applied electroantennography to determine which candidate chemicals were detected by the antennae of both summer and winter morphs. Behavioural bioassays were then performed to identify which chemicals repelled both morphs under laboratory conditions. A semi-field experiment was then conducted to determine whether chemicals identified as repellents in laboratory studies could reduce numbers of *D. suzukii* captured in traps baited sentinel fruit. Finally, trials were conducted in polytunnels to measure the distance over which repellent dispensers could reduce *D. suzukii* emergence in a covered strawberry crop.

2 MATERIALS AND METHODS

2.1 *Drosophila suzukii* cultures

Drosophila suzukii were from an Italian strain collected in 2013 and reared in the UK at NRI and NIAB East Malling for multiple generations. The colony was maintained as summer morphs in plastic tubes (10 × 2 cm^2 diam; Fisher Scientific, UK) and cages (30 × 30 × 30 cm^3; Bugdorm-1, NHBS Ltd, UK) at 25 ± 2 °C, 65% relative humidity (RH) under a 16 h:8 h, light:dark photoperiod. Juveniles and adults were fed on cornmeal media.[34] To produce winter morphs, stage three *D. suzukii* larvae were moved into a temperature-controlled cabinet (12 °C, 65% RH, 0 h:24 h, light:dark photoperiod), with adult winter morphs emerging after 6–8 weeks. Winter morphs exhibited higher levels of abdominal melanization than summer morphs as previously observed in the laboratory and field.[35] All adult summer and winter morphs used in experiments were 5–7 days post-eclosion.

2.2 Stimulus chemicals

Fourteen potential repellents for testing were selected from the literature and ongoing research at NIAB East Malling and NRI. The chosen chemicals comprised: three acetates (butyl acetate,[36] hexyl acetate,[36] heptyl acetate[37]), five other esters (ethyl propionate,[38] methyl anthranilate,[39] butyl anthranilate,[40] methyl salicylate,[41] methyl *N*,*N*-dimethylanthranilate[40]), two ketones (2-undecanone,[42] 2-tridecanone[42]), two alcohols (geosmin,[21] 1-hexanol[43]), one aldehyde (benzaldehyde[21]) and one amide (DEET[40]).

Hexyl acetate (98%; 142-92-7), heptyl acetate (98%; 112-06-01), butyl acetate (98%; 123-86-4), ethyl propionate (99%; 105-37-3), 2-undecanone (98%; 112-12-9), 2-tridecanone (96%; 593-08-8), 1-hexanol (98%; 111-27-3), DEET (97%; 134-62-3) and ethyl hexanoate (98%; 123-66-0): were purchased from Sigma-Aldrich (now Merck, Gillingham, Dorset, UK). Butyl anthranilate (98%; 7756-96-7) and methyl *N*,*N*-dimethylanthranilate (97%; 85-91-6) were obtained from Tokyo Chemical Industries (Oxford, UK). Methyl anthranilate (99%; 134-20-3) was purchased from Acros Organics, methyl salicylate (98%; 119-36-8) was purchased from Alfa-Aesar, and benzaldehyde (99%; 100-52-7) was bought from Lancaster Synthesis (all now Thermo Fisher Scientific, Horsham, UK). Geosmin (98%; 19700-21-1) was purchased from Hermitage Oils (Arezzo, Italy) as a 1% solution in diethylene glycol and purified (98%) by dissolving the solution (1 mL) in water (10 mL) and extracted twice in hexane (10 mL). The extracts were washed twice more with water (10 mL), dried with anhydrous magnesium sulfate, and assayed by gas chromatography against an internal standard of decyl acetate.

2.3 Electroantennograms

Electrophysiological responses of summer- and winter-morph antenna to potential repellents were measured using a procedure adapted from those used previously in studies of *D. suzukii*.[30] Individual female *D. suzukii* summer (gravid) or winter (nongravid) morphs were inserted into a 200-μL pipette tip (11 597 442; Thermo Fisher Scientific) with the thin tip removed such that the antennae and two-thirds of the head protruded. Cotton wool was placed at the posterior end of the fly to inhibit movement. The tip was mounted horizontally onto the EAG recording unit (AC/DC Amplifier UN-06; Syntech, the Netherlands; now Ockenfels Syntech GmbH, Buchenbach, Germany) such that the ventral surface of the fly faced upwards.

Ground and recording electrodes both consisted of a silver wire inserted into heat-pulled borosilicate glass (G150F-3; Harvard Apparatus, Bury St Edmunds, UK) filled with Beadle-Ephrussi Ringer solution and 1% polyvinylpyrrolidone (PVP). The reference electrode was cut at a 45° angle and inserted into the right eye with the recording electrode placed onto the posterior of the third segment of the left antenna. The DC output from the EAG probe was connected to an analogue-digital converter (IDAC 4; Syntech) and EAG responses recorded using AutoSpike 3.9 software (Syntech). The live insect preparation was placed under a constant flow of charcoal filtered humidified air (1 L min^{-1}) (CS-05, Stimulus Controller; Syntech).

The 14 test chemicals were diluted in liquid paraffin (Pure, Water White; Thermo Fisher Scientific). Ten microlitres of a 0.1 mg mL^{-1} solution of each test chemical (1 μg) were dispensed onto a strip of filter paper (40 × 5 mm) (11 582 003; Thermo Fisher Scientific) held within an unplugged Pasteur pipette (11 546 963; Thermo Fisher Scientific). The amount used (1 μg) was chosen to ensure that sufficient test chemical reached the insect antenna regardless of differences in compound volatility. The wide end of the pipette was connected to an air supply (0.3 L min^{-1}) which could be switched on and off via a footswitch on the stimulus controller.

Test chemicals were puffed over the antennal preparation by inserting the end of the glass pipette into a small hole in the stainless-steel air delivery tube (internal diameter 12 mm). Puff duration was 0.5 s. A maximum of five test chemicals was presented to a single *D. suzukii*, and the order in which the chemicals were presented was rotated between flies. A control stimulus of liquid paraffin was puffed before and after each experimental stimulus, and 60 s was left between each puff to allow for antennal recovery. Each chemical was presented to 10 separate *D. suzukii* summer and winter morphs. Each replicate run lasted a maximum of 15 min. The first and last chemical presented over the antenna was a known stimulant[44] (ethyl hexanoate, 98%; 123-66-0; Merck) used at the same chemical concentration as the repellents to check for a reduction in EAG response resulting from antennal fatigue.[45]

A one-sample Mann–Whitney *U*-test was used to identify which of the potential repellents elicited an adjusted EAG response[45] (relative to the responses elicited by the paraffin control) that was significantly different from 0 mV in each of the two morphs. A two-sample Mann–Whitney U-test was used to compare the magnitude of corrected responses elicited by each test chemical in *D. suzukii* summer and winter morphs. Adjusted responses to ethyl hexanoate at the beginning and end of each run were compared using Wilcoxon signed-rank tests. All analyses were performed in R (v4.0.2).[46]

2.4 Laboratory bioassays

Behavioural responses to potential repellents were measured using modified gated-trap choice tests[21] at NRI in a temperature-controlled environment (25 ± 1 °C, 60 ± 5% RH, 16 h:8 h, light:dark photperiod). A 1-L plastic cup was used as a bioassay arena (14 × 10 cm^2) (1 L Microlite; Cater4You, High Wycombe, UK), with a mesh lid (Microlite lid; Cater4You). Damp filter paper (area 8 cm^2) was added to the arena floor to maintain ambient humidity and reduce insect mortality. Two lidded gated traps were placed within the arena. The traps were 29-mL pots (5 × 5 cm^2) with plastic lids (DPCL100; Donovan Bros Ltd, Orpington, UK). A 2.5-mL pipette tip (11 507 462; Thermo Fisher Scientific) was inserted into the lid via a cut hole (6 mm) as an entry point for the *D. suzukii*. An insect pin (E6850; Watkins and Doncaster, Leominster, UK) was inserted through the lid to hold a 2 cm^2 piece of filter paper onto which control or test chemicals could be dispensed. Each trap contained 5 mL attractive bait [1000 g crushed raspberries, deionized water up to 2 L and 130 g of Allison easy bake yeast (Allison Flour, UK)][21] and a drop of non-scented detergent to disrupt surface tension and prevent trapped flies from escaping (Zero%washing up liquid; Ecover Direct, UK).

One trap in each arena was treated with a test chemical in hexane (6 μL; 10^{-1}, 10^{-2}, or 10^{-3} v/v) on the filter paper. The other trap received hexane only (6 μL). A range of doses was tested as *D. suzukii* responses to semiochemicals can vary with amount presented.[21] After 10 min to allow the hexane to evaporate, trap lids were replaced and 10 female *D. suzukii* winter or summer morphs were introduced into the arena via a 10-mm hole in the arena lid. Each experimental replicate began at 09:30 h and ran for 24 h after which numbers of *D. suzukii* in each gated trap were counted. Flies were starved for 17 h before all experiments. Ten replicates were performed for each test chemical dilution using *D. suzukii* summer and winter morphs. In addition, a positive control experiment was conducted to confirm that greater numbers of *D. suzukii* were attracted to the raspberry and yeast bait compared to deionized water when presented in the same arena ($n = 10$).

A Repellency Index was calculated for each dose of each chemical tested as: number of *D. suzukii* in the control trap (no repellent) minus the number of *D. suzukii* in the test trap (with repellent). Indices were calculated separately for summer- and winter-morph *D. suzukii*. A one-sample Wilcoxon test was used to identify which doses of each chemical elicited a Repellency Index significantly different from zero.

2.5 Formulation of test chemicals for semi-field studies

Four chemicals which demonstrated efficacy in laboratory bioassays, ethyl propionate, methyl *N*,*N*-dimethylanthranilate, DEET and benzaldehyde, were formulated into controlled-release dispensers for semi-field trials. Each test chemical (500 mg) was dispensed onto a cotton dental roll (14 × 6 mm; Kent Express Dental Supplies, Gillingham, UK) in a sachet prepared from polyethylene lay-flat tubing (50 × 50 × 120-μm thick; SPK 230; Audion Elektro, Derby, UK) which was then heat-sealed. Control dispensers were constructed likewise but without test chemicals. This amount of chemical used (500 mg) was chosen to allow for continued release of test chemical throughout the experiment. Dispenser release rates were measured through daily changes in weight when maintained at 20–22 °C in a laboratory fume hood at NRI.

2.6 Semi-field trapping studies

Trapping studies were conducted in polytunnels at NIAB East Malling to measure the efficacy of potential repellents under semi-field conditions. Each of 12 polythene tunnels (12 × 2.15 × 1 m high) were covered with an outer layer of insect exclusion netting and an inner layer of green scrim netting (12 × 2 m), the latter to provide shade for *D. suzukii* (Fig. S1). One red Droso Trap (Biobest Group NV, Westerlo, Belgium) was placed 100 cm from either end of the polytunnel and 20 cm aboveground on white packing crates (50 × 30 × 20 cm^3). Each trap was surrounded by five test chemical dispensers and positioned in a grid with 50 cm spacing between dispensers (Fig. S2). One of the five dispensers was attached to the outside of the Droso Trap lid. Control dispensers (with no chemicals) were placed in the same configuration around the second Droso Trap. Six ripe raspberries (Driscoll's Maravilla) were placed into each of the two Droso Traps in each polytunnel as bait and oviposition substrate. Preliminary toxicity tests were used to ensure the fruit was not contaminated with insecticide residues (<20% *D. suzukii* mortality over 48 h; data not shown).

For each replicate, 100 *D. suzukii* were released from white delta traps without sticky bases (Russell IPM, Deeside, UK), suspended at a height of 200 cm in the centre of each polytunnel (Fig. S2). The delta trap provided a resting surface and shade for the *D. suzukii* at the start of each experiment. After 48 h the Droso Traps were opened, and trap catch removed. The flies were placed into the freezer for 1 h, confirmed as *D. suzukii*[47] and counted. Raspberries were removed from the sentinel traps, placed into individual emergence boxes, and stored in a temperature-controlled environment (~22 ± 2 °C, >40% RH, 16 h:8 h, light:dark photoperiod). After 14 days, emerging *D. suzukii* were removed using an aspirator connected to pump (DA7C; Charles Austen, Surrey, UK) and counted.

Twelve replicates were performed in total for each test chemical plus a control-only treatment (both traps with dispensers without test chemicals, with the designated test side alternated between replicates). Twelve replicates were performed using *D. suzukii* summer morphs (April–May) and 12 using winter morphs (September–October). Polytunnels were left empty for 48 h between runs and positions of test and control traps within each polytunnel alternated between replicates.

For each chemical tested a Repellency Index was derived as for laboratory bioassays (number of *D. suzukii* caught in control traps – number caught in traps surround by test chemical dispensers per replicate). One-sample Wilcoxon tests were used to determine which chemicals elicited a Repellency Index significantly different from zero. Wilcoxon tests also were used to determine whether there was a significant difference in numbers of *D. suzukii* emerging from traps with and without test chemical dispensers, and if there were significant differences in the ratio of flies emerging per adult flies captured between test and control traps. For the latter test, only those replicate pairs where ratios could be derived (i.e. nonzero numbers of *D. suzukii* caught in each trap) were retained for analysis.

2.7 Polytunnel trials in a strawberry crop

A second semi-field trial was performed in a strawberry crop. The objectives were to determine whether repellents could reduce the total number of *D. suzukii* emerging from fruit and the distance over which the chemicals could deter oviposition. Ethyl propionate, methyl *N*,*N*-dimethylanthranilate, benzaldehyde and a blank control were formulated in dispensers as above.

Twenty coir bags (50×20 cm^2), each planted with eight cv. Amesti strawberry plug plants were placed into the polytunnels described above. Bags were held 20 cm off the ground on white plastic packing crates ($50 \times 30 \times 20$ cm^3). Each strawberry plant held between five and seven strawberries. Additional strawberries were picked between experiments such that numbers of fruit were comparable between polytunnels.

Five repellent dispensers were placed at one end of the polytunnel and positioned in a grid with 50-cm spacing between dispensers. For each replicate, 15 male and 15 mated female summer-morph *D. suzukii* were released from a white delta trap (Russell IPM) suspended at the centre of each polytunnel. Fruits were sampled for *D. suzukii* on Day 7 post release. Six ripe strawberries were picked from seven sampling points at distances of 0, 1, 3, 5, 7, 9 and 11 m from the dispensers. Fruits were placed into individual emergence boxes and incubated in a temperature-controlled environment (22 ± 2 °C, >40% RH, 16 h:8 h, light:dark photoperiod) for 14 days and numbers of SWD emerging were assessed as above. Twelve replicates were performed for each test chemical and the control between June and August 2020. In the final summer trial, numbers of *D. suzukii* larvae in polytunnels were reduced between sets of replicates by picking ripe fruit on days one and five after the completion of a replicate and using red Droso Traps baited with Droso Lure to trap surviving adult *D. suzukii*. Traps were removed 24 h before the next experimental replicate. Position of dispensers in polytunnels was alternated between replicates.

A general linear model in R was used to determine whether total numbers of *D. suzukii* emerging from fruit were different between chemical treatments, The total numbers of *D. suzukii* emerging from fruit collected from each polytunnel was summed, transformed to (log+1) and entered into the model as a dependent factor. Treatment (control or dispensers loaded with each of the three test chemicals) was entered as the independent variable. Tukey's honestly significant difference (HSD) tests were used to identify significant differences between individual treatments.[48]

General linear mixed models[49] were used to assess whether distance from the control or treatment dispensers had a significant effect on numbers of *D. suzukii* emerging from fruit in polytunnels. For each treatment, the number of *D. suzukii* emerging at each distance transformed to (log+1) was entered as the dependent variable in the model, and distance from the dispensers (0, 1, 3, 5, 7, 9, and 11 m) entered as a fixed factor. Replicate (12 per treatment) was entered as a random effect. Overall effect of distance in the models was assessed using *F*-tests, with Tukey's HSD tests on estimated marginal means[48] were used to compare numbers of *D. suzukii* emerging at each distance.

3 RESULTS

3.1 Electroantennograms

All 14 chemicals tested elicited a significant EAG response in the antenna of *D. suzukii* summer and winter morphs at the single dose tested (1 μg; Table 1). Hexyl acetate and geosmin both elicited a significantly greater corrected EAG response in summer morphs than winter morphs (Table 1). There also was a tendency toward greater EAG responses in summer morphs than winter morphs to heptyl acetate and 1-hexanol, although these differences were not significant at $P < 0.05$ (Table 1). Corrected responses varied from 0.10to 1.14 mV, but comparisons of the magnitudes of EAG responses are confounded by the wide variation in volatilities of the compounds tested and hence the amounts of material impacting on the antennae under the experimental conditions. There was no overall significant difference in corrected response to the ethyl hexanoate control presented at the beginning and end of each run (Wilcoxon test, summer morphs; $P = 0.51$; winter morph; $P = 0.39$).

3.2 Responses of *Drosophila suzukii* summer and winter morphs to 14 chemicals in behavioural bioassay

A greater number of *D. suzukii* summer morphs were attracted to the fruit juice compared to the deionized water control; the median difference in *D. suzukii* attracted to fruit juice compared to control was 7.0 (interquartile range IQR 6.0–8.0; Wilcoxon test, $n = 10$, $P < 0.01$). Likewise, more *D. suzukii* winter morphs were attracted to the fruit juice compared to the control with median difference 7.0 (IQR 6.0–10.0; Wilcoxon test, $n = 10$, $P < 0.01$).

Summer-morph *D. suzukii* were repelled by seven of the chemicals tested at one or more doses used in laboratory bioassays (Fig. 1). Butyl acetate, ethyl propionate, methyl *N*,*N*-dimethyl anthranilate and geosmin were repellent at 0.1 v/v. Methyl salicylate and DEET were repellent at all doses tested. Benzaldehyde was repellent at 0.001 v/v and 0.1 v/v. All other chemicals tested had no significant effect on summer-morph behaviour.

Winter-morph *D. suzukii* were repelled by six of the chemicals tested (Fig. 2). Ethyl propionate, methyl anthranilate and methyl *N*,*N*-dimethyl anthranilate were repellent at 0.1 v/v. DEET was repellent at all doses tested. Benzaldehyde was repellent at 0.1 v/v and 0.01 v/v. Butyl anthranilate was repellent at 0.01 v/v. All other chemicals tested had no significant effect on winter-morph behaviour.

Table 1. Electroantennogram responses of *Drosophila suzukii* summer and winter morphs to 14 potential repellent chemicals (1 µg dose; *n* = 10)

	Chemical	Mean (IQR) corrected EAG response (mV)†		Difference between morphs‡
		Summer morph	Winter morph	*P*-value
Acetates	Butyl acetate	1.04 (1.0–1.4)**	0.77 (0.4–1.2)**	0.32
	Hexyl acetate	0.46 (0.4–0.7)**	0.22 (0.2–0.2)**	0.03*
	Heptyl acetate	0.40 (0.3–0.7)**	0.18 (0.1–0.3)**	0.06
Esters	Ethyl propionate	1.14 (0.9–1.7)**	0.95 (0.7–1.0)**	0.11
	Methyl anthranilate	0.70 (0.3–1.3)**	0.91 (0.7–1.0)**	0.65
	Butyl anthranilate	0.73 (0.6–1.0)**	0.95 (0.9–1.0)**	0.12
	Methyl salicylate	0.65 (0.3–0.7)**	0.55 (0.4–0.7)**	0.63
	Methyl *N*,*N*-dimethyl-anthranilate	0.33 (0.2–0.6)**	0.28 (0.1–0.5)**	0.42
Ketones	2-Undecanone	0.18 (0.1–0.2)**	0.10 (0.1–0.2)**	0.43
	2-Tridecanone	0.19 (0.1–0.3)**	0.11 (0.1–0.3)*	0.50
Alcohols	Geosmin	0.56 (0.5–0.7)**	0.15 (0.1–0.3)**	0.005**
	1-Hexanol	0.88 (0.6–1.2)**	0.49 (0.3–0.6)**	0.05
Aldehydes	Benzaldehyde	0.45 (0.3–0.5)**	0.45 (0.1–0.8)**	0.87
Amides	DEET	0.20 (0.1–0.3)**	0.23 (0.2–0.4)**	0.32

† Significance of corrected EAG responses compared to 0 mV (one-sample Wilcoxon test).
‡ Mann–Whitney *U*-test.
**P* < 0.05;
** *P* < 0.01.

Overall, four chemicals were repellent against both the summer and winter morphs in the laboratory: ethyl propionate, methyl *N*,*N*-dimethylanthranilate, benzaldehyde and DEET.

3.3 Formulation of test chemicals

Dispensers loaded with 500 mg ethyl propionate released material for 2 days only at 160–320 mg day^{-1} (Fig. S3). Release from benzaldehyde dispensers followed an asymptotic curve, with release approximately linear at 45 mg day^{-1} for the first 4 days (Fig. S3). Dispensers loaded with methyl *N*,*N*-dimethyl anthranilate released ~3.7 mg day^{-1} for the duration of the experiment (Fig. S3). DEET was released relatively slowly from dispensers at <0.5 mg day^{-1} (Fig. S3).

3.4 Semi-field trapping studies

No significant differences were found in numbers of summer or winter morphs of *D. suzukii* caught in traps surrounded by empty dispensers compared to paired control traps (one sample Wilcoxon tests; Fig. 3). Significantly fewer summer and winter morphs were collected in traps surrounded by ethyl propionate dispensers than paired control traps (one sample Wilcoxon tests; Fig. 3). Traps surrounded with dispensers releasing methyl *N*,*N*-dimethylanthranilate and benzaldehyde also caught fewer summer and winter morphs than paired controls (one sample Wilcoxon tests; Fig. 3). No significant difference was found between numbers of summer or winter morphs caught in traps surrounded by DEET dispensers than paired controls (one sample Wilcoxon tests; Fig. 3).

No difference was found in the numbers of *D. suzukii* emerging from fruit in traps surrounded by empty dispensers compared to control traps for either summer or winter morphs (Wilcoxon test; Fig. S4). Significantly fewer flies emerged from fruit from traps surrounded by ethyl propionate than from the paired control for summer morphs of *D. suzukii* (Fig. S4), but there was no evidence of a similar effect on winter morphs. Emergence from fruit in traps surrounded by dispensers loaded with methyl *N*,*N*-dimethylanthranilate and benzaldehyde was lower for both summer and winter morphs (Fig. S4). There was no effect of DEET dispensers on emergence of *D. suzukii* summer or winter morphs (Fig. S4). Correcting for numbers of adults caught in each trap there was no significant effect of any treatment on emergence (Wilcoxon test; Fig. S5).

3.5 Polytunnel trials in a strawberry crop

A significant overall difference was found between treatments in total numbers of *D. suzukii* emerging from fruit in polytunnels ($F = 4.9$, df = 3, 44, $P < 0.01$; Fig. 4). Significantly fewer *D. suzukii* emerged from tunnels treated with ethyl propionate dispensers compared to controls (Tukey's HSD test on estimated marginal means, $P < 0.05$). Total numbers of *D. suzukii* emerging from tunnels treated with benzaldehyde and methyl *N*,*N*-dimethylanthranilate were not significantly different from numbers emerging from control tunnels or tunnels treated with ethyl propionate dispensers (Tukey's HSD test; Fig. 4).

In control tunnels, there was no significant effect of distance from dispensers in numbers of *D. suzukii* emerging from fruit ($F = 0.1$, df = 6, 72, $P = 0.99$; Fig. 5, top left). In tunnels treated with benzaldehyde there was a significant effect of distance on numbers of *D. suzukii* emerging from fruit ($F = 2.8$, df = 6, 72, $P = 0.02$), but the only significant individual difference was found between numbers of *D. suzukii* emerging at 7 and 11 m (Fig. 5, top right). A significant effect of distance was found in tunnels treated with ethyl propionate ($F = 23.9$, df = 6, 72, $P < 0.001$), with numbers emerging at 0, 1, and 3 m significantly lower than at 5 m (Fig. 5, bottom left). A significant effect of distance also was found in tunnels treated with methyl *N*,*N*-dimethylanthranilate ($F = 51.64$, df = 6, 72, $P < 0.001$). Numbers emerging at 0, 1, and 3 m were significantly lower than at 5 m, and numbers emerging at 5 m significantly lower than at 7 m (Fig. 5, bottom right). For each test chemical treatment, a decrease was observed in numbers of *D. suzukii* emerging at the opposite end of the tunnel from

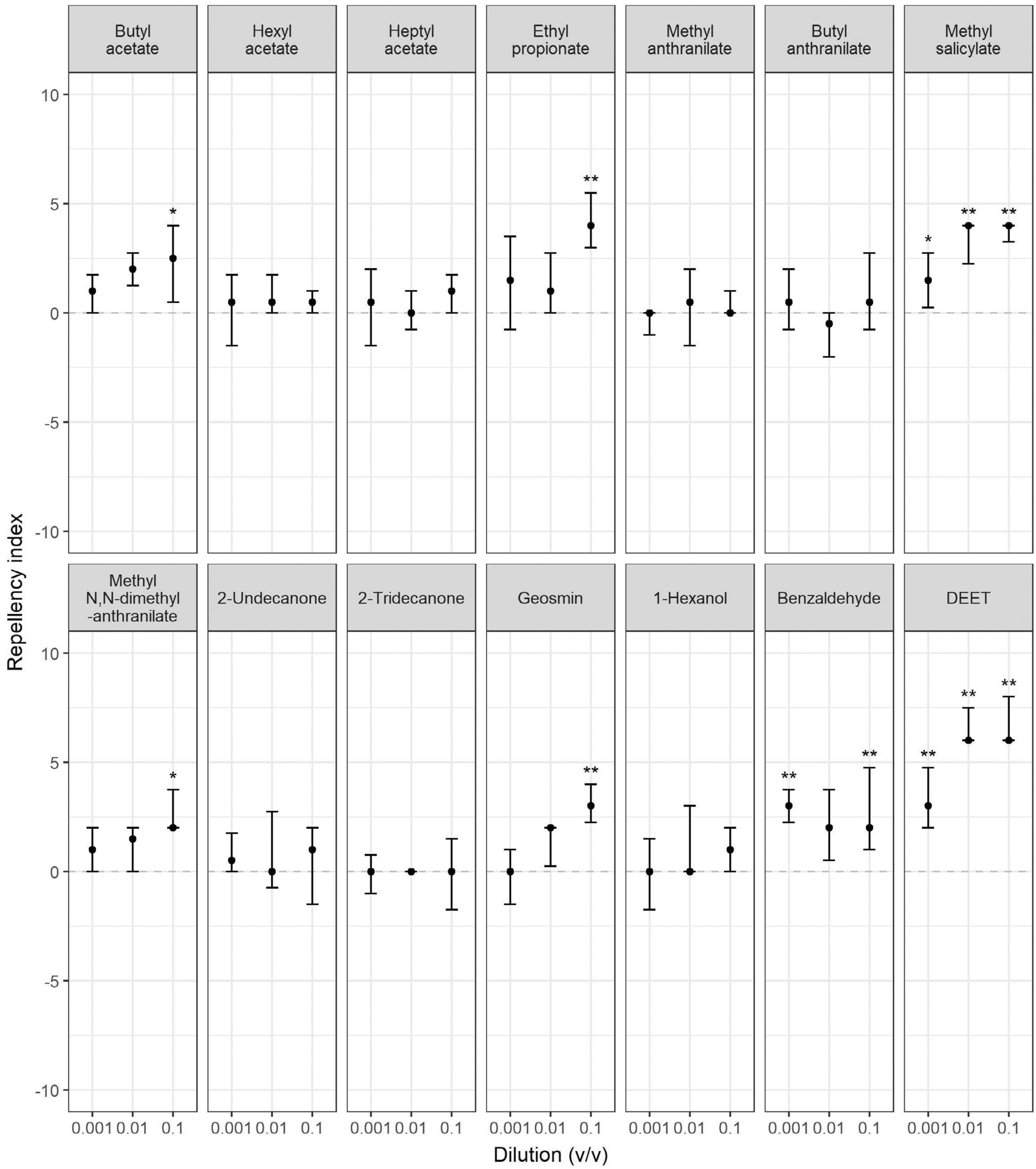

Figure 1. Median (± IQR) responses of *Drosophila suzukii* summer morphs to 14 test chemicals in laboratory bioassays. Repellency Index calculated as number of *D. suzukii* caught in trap without repellent – number caught in trap with repellent per replicate. *,$P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$ (index significantly different from zero, one-sample Wilcoxon test).

the dispensers, at the furthest point from which adults were released into the tunnel (Fig. 5).

4 DISCUSSION

This study has demonstrated the potential efficacy of ethyl propionate and methyl *N,N*-dimethylanthranilate dispensers as repellents for protecting crops against *D. suzukii* under semi-field conditions. Numbers of *D. suzukii* summer morphs emerging from fruits were significantly reduced to very low levels within 3–5 m of dispensers releasing ethyl propionate or methyl *N,N*-dimethylanthranilate. Furthermore, significantly fewer *D. suzukii* overall emerged from fruit in polytunnels treated with ethyl propionate dispensers compared to controls. With methyl *N,N*-

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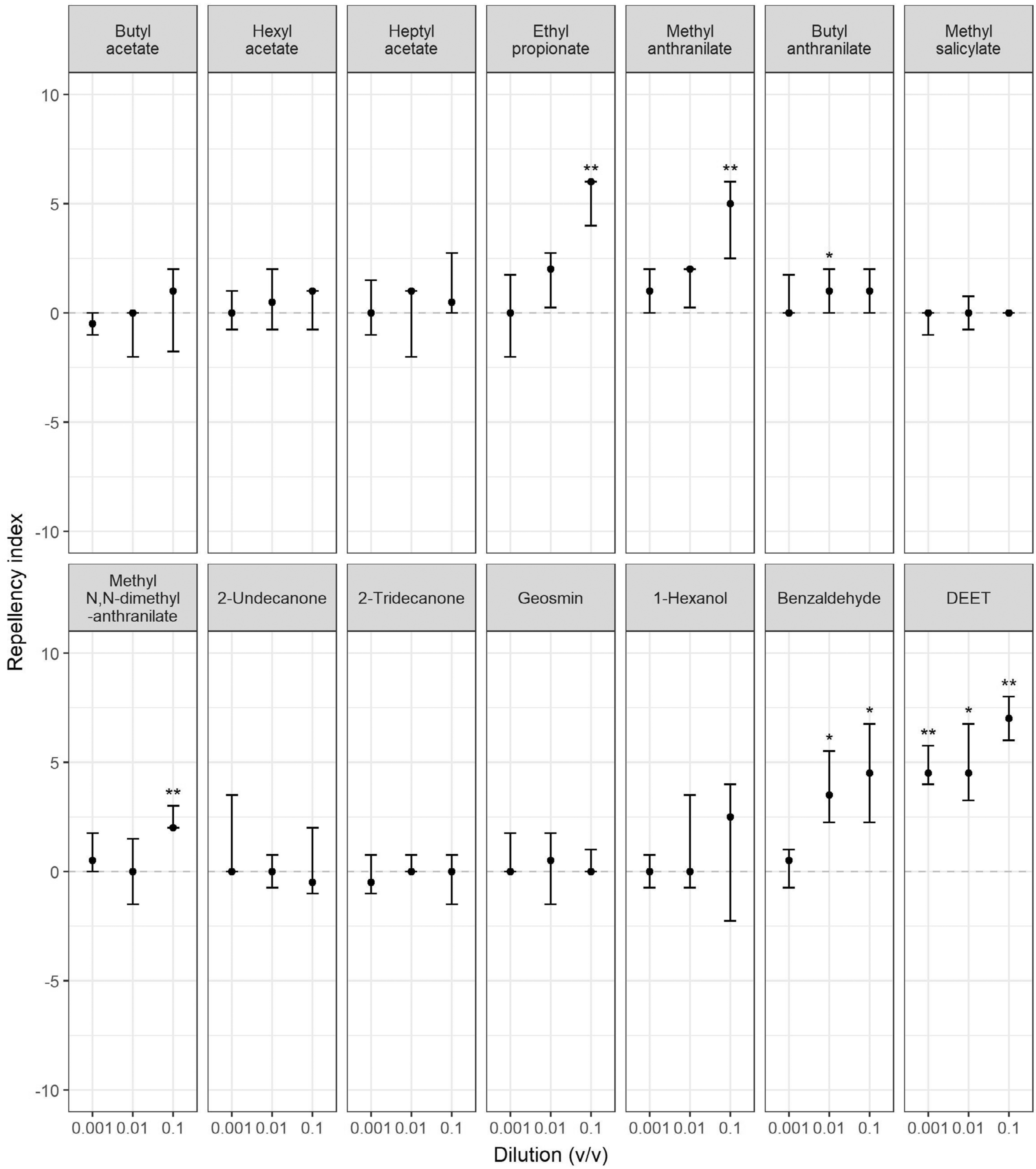

Figure 2. Median (± IQR) responses of *Drosophila suzukii* winter morphs to 14 test chemicals in laboratory bioassays. Repellency Index calculated as number of *D. suzukii* caught in trap without repellent – number caught in trap with repellent per replicate. *,$P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$ (index significantly different from zero, one-sample Wilcoxon test).

dimethylanthranilate, overall numbers of *D. suzukii* emerging were reduced but not significantly so. Results of trapping experiments in the absence of a crop indicated that these repellents also may be effective against the *D. suzukii* winter morph. For both summer and winter morphs, numbers in traps surrounded by repellents were lower than those without repellents. However, in this experiment there was no effect on oviposition in that, when corrected for numbers of adults attracted, numbers of adults subsequently emerging from fruit in the traps with or without repellents were not significantly different.

Ethyl propionate is produced by many ripening fruits and has previously been identified as a component of volatile blends

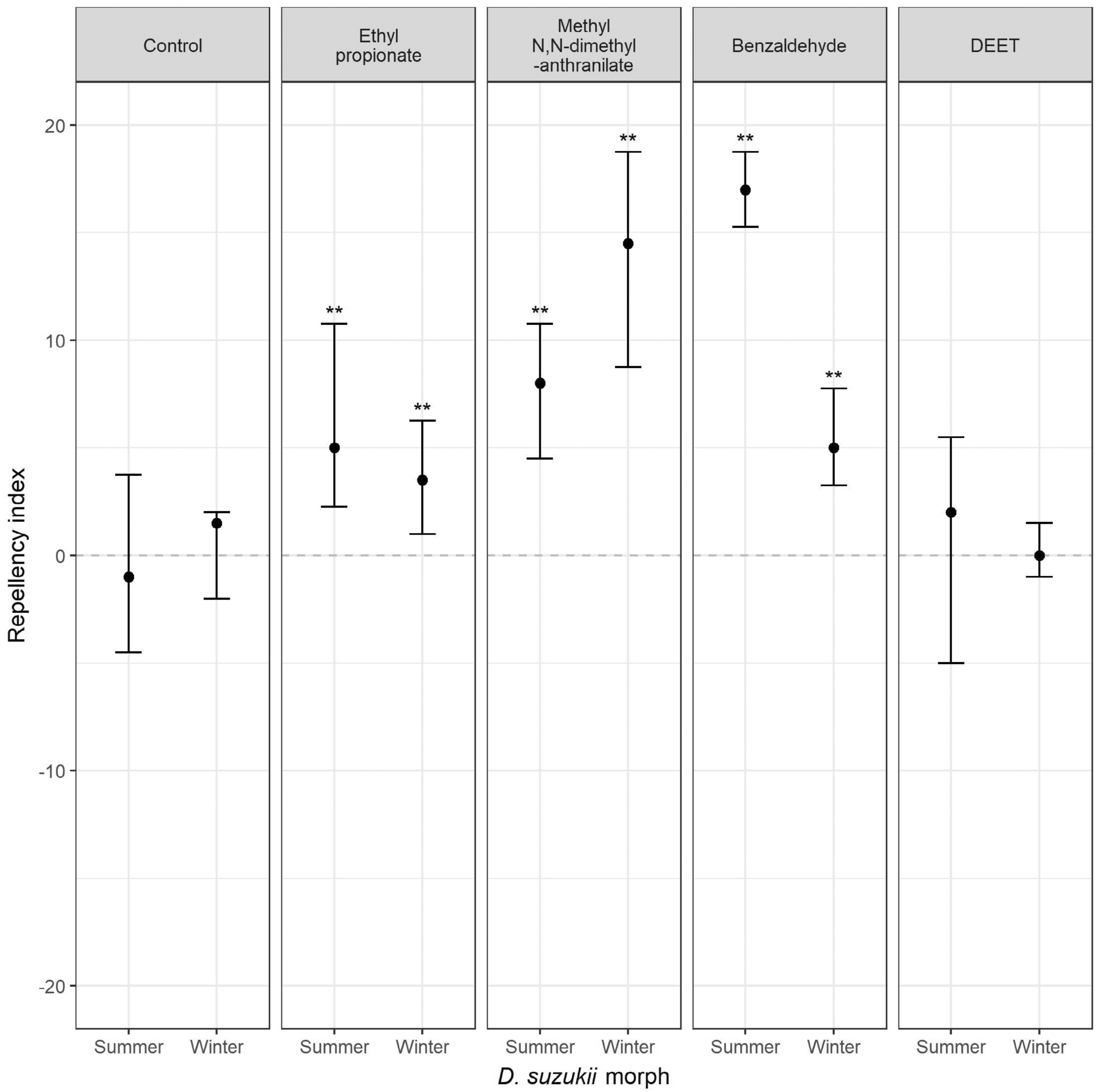

Figure 3. Median (± IQR) responses of *Drosophila suzukii* summer and winter morphs to three test chemicals in polytunnel trapping studies. Repellency Index calculated as number of *D. suzukii* caught in traps without repellent dispensers – number caught in traps surrounded by repellent dispensers. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$ (index significantly different from zero, one-sample Wilcoxon test).

attractive to the Queensland fruit fly *Bactrocera tryoni*.[50] Behavioural responses of *D. suzukii* to ethyl propionate have not been investigated previously, and the results of the current study indicate that this chemical reduces attraction of both summer and winter morphs towards fruit and fruit juice baits, possibly over several metres from the point of release. A reduction in total numbers of *D. suzukii* emerging from fruit in polytunnels treated with ethyl propionate was observed, but this effect was not apparent in the experiment with traps surrounded by repellent dispensers at 0.5 m. Further work is needed to examine the direct effect of ethyl propionate on oviposition by *D. suzukii*, and the ecological significance of the apparent repellent effect of this ripening fruit volatile.

Methyl *N*,*N*-dimethylanthranilate is considered a potentially safer substitute for DEET as a general insect repellent, which has previously been shown to repel *D. suzukii* in the laboratory.[40] This chemical may be more appropriate for commercial use than ethyl propionate as ethyl propionate was released quickly from dispensers over 2 days under laboratory conditions, but linear release of methyl *N*,*N*-dimethylanthranilate was observed for ≥25 days. Minimizing the labour required for replacing dispensers will be critical to the viability of using repellents for protecting

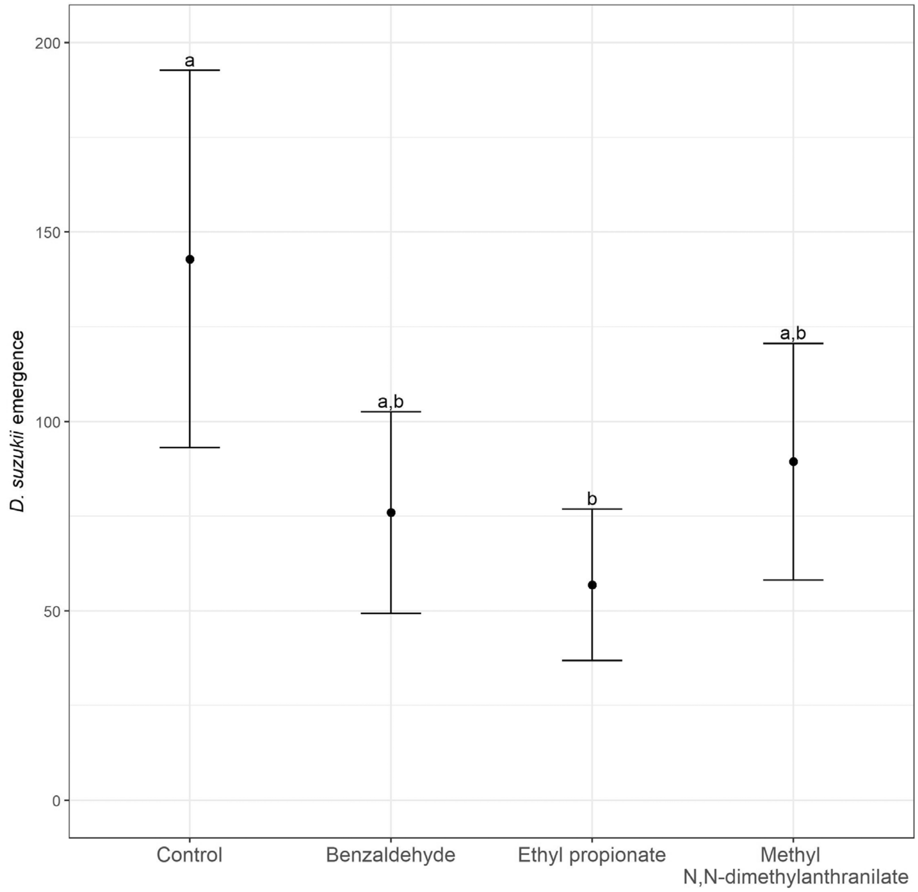

Figure 4. Mean (± 95% confidence intervals) numbers of *Drosophila suzukii* summer morphs emerging from fruit collected from polytunnels treated with three potential repellents and a control. Means and confidence intervals derived from a general linear model on data transformed to log(x + 1). Treatments with different letters are significantly different ($P < 0.05$, Tukey's HSDtest on estimate marginal means).

crops from *D. suzukii*. DEET repelled both the summer and winter morph at all doses tested in the laboratory, but was not taken forward for field testing, in part aas a consequence of difficulties in formulating this solid into a suitable slow-release dispenser.

Benzaldehyde was effective in reducing attraction of both summer and winter morphs from fruit baited traps under laboratory and semi-field conditions but was not found to act as a repellent in the presence of a strawberry fruit crop. In a previous laboratory study,[21] benzaldehyde was not found to be effective as a repellent against *D. suzukii*, even though it is considered a strong aversive odour for *D. melanogaster*.[21] Differences in experimental methodologies may explain these apparent discrepancies.

All 14 chemicals tested elicited electrophysiological responses in the antennae of both summer- and winter-morph *D. suzukii*, indicating that both morphs possess olfactory receptors capable of binding to these compounds at the dose rates presented. Geosmin elicited a significantly larger corrected EAG response in the summer morph than in the winter morph, as reported previously.[30] Responses to hexyl acetate also were greater in summer morphs. EAG is not a reliable quantitative technique, as response magnitude can vary with aspects of the biological preparation and test chemical volatility. Differences in responses to individual chemicals observed here and previously[30] might be indicative of specific differences between morphs in the peripheral olfactory system. Single sensillum recordings are required to elucidate whether there are differences in numbers and types of olfactory receptor neurones between morphs, which might explain chemical-specific differences in EAG responses between morphs.[30]

Differences also were observed in the behaviour of summer and winter morphs to several compounds in gated-trap bioassays. Geosmin repelled summer morphs at the highest dose tested while no effect was found on winter morphs. Similar differences in responses of the two morphs to this chemical have been reported in no choice and T maze bioassays.[30] Geosmin may not only signal the presence of harmful soil microorganisms and sites unsuitable for oviposition, but also indicate suitable habitats in which winter-morph *D. suzukii* could overwinter.[30,51] Geosmin was found not to be effective in repelling summer morphs in previous semi-field studies[21,23] and was not tested further here.

Methyl salicylate repelled summer morphs but not winter morphs in laboratory bioassays. Released from strawberries through insect feeding, methyl salicylate may act in plant defence by repelling herbivores and attracting predators.[52] It may therefore be more ecologically relevant to the ovipositing *D. suzukii* summer morph than to the winter morph. The plant defence compounds 2-undecanone and 2-tridecanone did not repel either morph in laboratory bioassays. Butyl acetate also repelled summer-morph *D. suzukii* in the laboratory but had no effect on

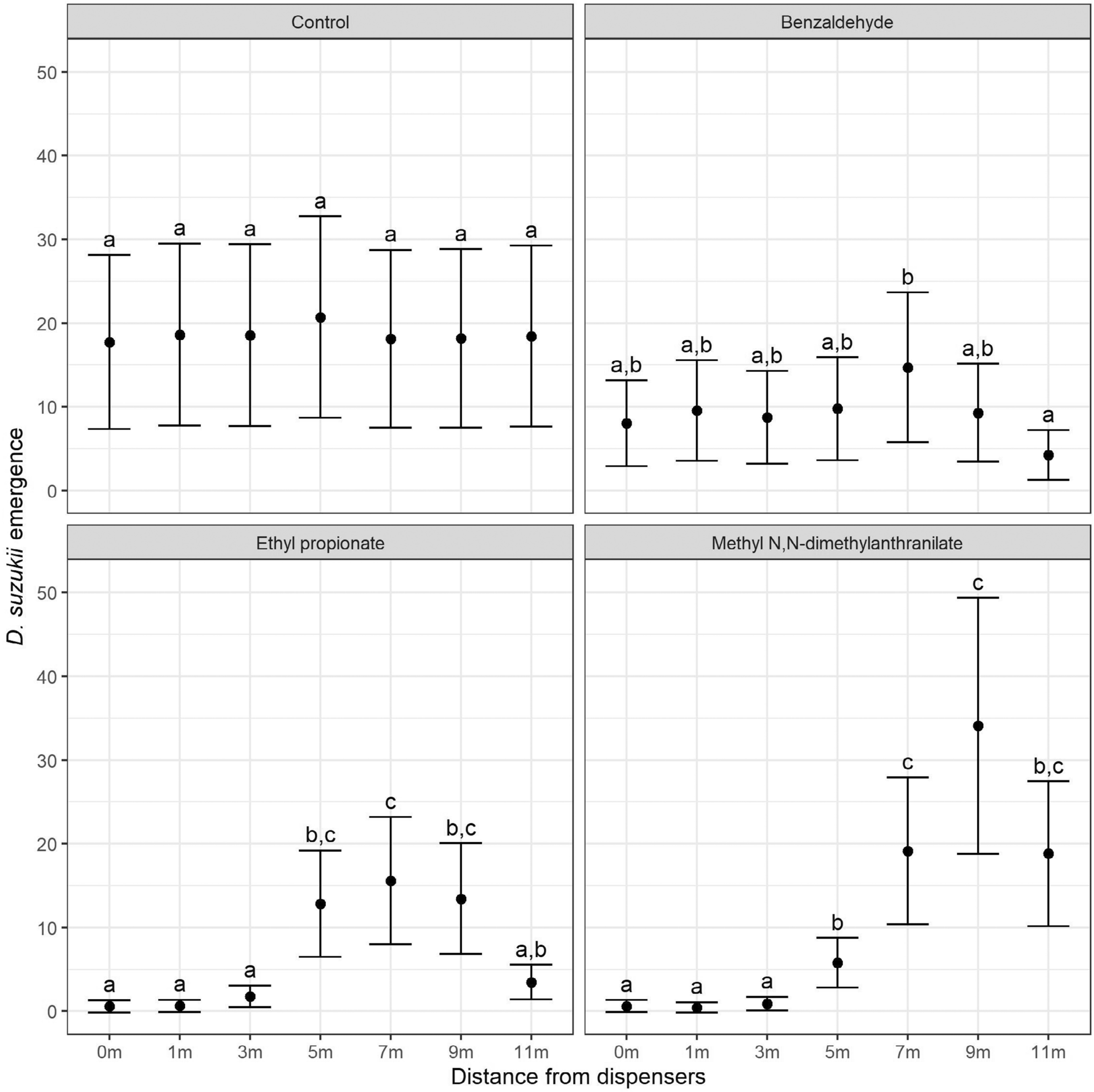

Figure 5. Mean (± 95% confidence intervals) numbers of *Drosophila suzukii* emerging from fruit collected from polytunnels at different distances from chemical dispensers. Means and confidence intervals derived from a general linear model on data transformed to log(x + 1). Treatments with different letters are significantly different ($P < 0.05$, Tukey's HSD test on estimate marginal means). Ovipositing *D. suzukii* were released into the tunnels at the mid-point (5 m).

the winter morph at the doses tested. Identified from headspace of ripening fruit[38,53] and fermentation products,[38,53,54] the effect of butyl acetate on *D. suzukii* behaviour remains unclear, despite several studies.[36,53,54] The results presented here may suggest that responses may be affected by fly physiological status. Methyl anthranilate repelled winter-morph *D. suzukii* but had no effect on summer morphs at doses tested. Identified from the head space of strawberries, methyl anthranilate is lethal to *D. suzukii* embryos and may play a role in plant resistance to this pest.[39] Behavioural responses of the adult summer morph to methyl anthranilate in the laboratory vary from attraction to aversion depending on dose.[39] The current study is the first to report a behavioural response of the winter morph to this same chemical. Butyl anthranilate, proposed as a potentially safer alternative to DEET for agricultural use, has previously been shown to be aversive to *D. suzukii*.[40] Here, butyl anthranilate only repelled winter morphs at one of the doses tested in laboratory bioassays and had no effect on the behaviour of summer morphs. This chemical was therefore not taken forward for field trials. Butyl anthranilate applied directly to fruit may reduce oviposition[40] yet also could affect the taste, and therefore value, of the crop. The release of volatile chemicals from dispensers, as tested here, may provide protection against *D. suzukii* through spatial repellency, avoiding the need to apply chemicals directly to marketable fruit.

5 CONCLUSION

Our results indicate that ethyl propionate and methyl *N,N*-dimethylanthranilate, formulated in appropriate dispensers, have potential for use in protecting fruit crops from *D. suzukii*. Responses of *D. suzukii* in laboratory and semi-field trapping studies indicate that these chemicals function as repellents, reducing the attractiveness of fruit baits. Further research is needed to determine the most appropriate release rates, and most cost-effective methods of formulation and deployment, of these technologies at a commercial scale in a range of crops attacked by *D. suzukii*. This should include testing repellents in combination with commercially available attractants within an integrated 'push-pull' strategy,[13,19] and exploring whether formulations can be varied to account for behavioural differences between summer and winter morphs.

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CONFLICT OF INTEREST

None.

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

Christina Conroy, Michelle T. Fountain, Daniel P. Bray, E. Charles Whitfield, and David R. Hall conceptualized the studies and assisted with practical work. Christina Conroy conducted all laboratory and field experiments. Christina Conroy and Daniel P. Bray drafted the manuscript and conducted statistical analyses. David R. Hall, Michelle T. Fountain, and E. Charles Whitfield had significant input into the writing of the final manuscript. Dudley Farman and David R. Hall purified chemicals used in the study and formulated them into release devices.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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