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SPOTTED WING DROSOPHILA, *DROSOPHILA SUZUKII* (DIPTERA: DROSOPHILIDAE), TRAPPED WITH COMBINATIONS OF WINES AND VINEGARS

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ABSTRACT

Field trapping experiments evaluated wine and vinegar baits for spotted wing drosophila flies, *Drosophila suzukii* (Matsumura), and assessed variance in bait attractiveness with wine type, vinegar type, and bait age. A mixture of apple cider vinegar and a Merlot wine attracted more flies than a mixture of acetic acid and ethanol. The vinegar/wine mixture attracted numbers of flies that were similar to numbers of flies trapped with acetic acid with wine or ethanol with vinegar. These results indicate that chemicals in vinegar in addition to acetic acid, and chemicals in wine in addition to ethanol, are attractants for the spotted wing drosophila. Numbers of flies captured with wine/vinegar mixtures varied somewhat with wine type, with a Merlot wine yielding best captures among the wines tested. Numbers of flies captured with wine/vinegar mixes also varied somewhat with vinegar type, with a rice vinegar yielding best captures among vinegars tested. Numbers of flies captured varied little with bait age, from 0 to 7 days old. These results will assist efforts to improve baits used to trap spotted wing drosophila, and to provide guidance for the isolation and identification of chemical attractants from wines and vinegars.

Key Words: attractants, detection, lures, monitoring, spotted wing drosophila, traps

RESUMEN

Se evaluó el uso de cebos de vino y de vinagre en experimentos de campo para atrapar moscas drosófilas de alas manchadas, *Drosophila suzukii* (Matsumura), y se evaluó la variación en la atractividad del cebo en cuanto al tipo de vino, el tipo de vinagre, y la edad del cebo. Una mezcla de vinagre de sidra de manzano y un vino Merlot atrae más moscas que una mezcla de ácido acético y etanol, y atrajo un número similar de moscas al atraído por el ácido acético con vino o con vinagre de etanol. Estos resultados indican que los productos químicos en vinagre, además de ácido acético y sustancias químicas en el vino, incluyendo el etanol, son atrayentes para la mosca drosófila de alas manchadas. El número de moscas capturadas con mezclas de vino / vinagre variaron un poco con el tipo de vino, la mejor en captura de moscas entre los vinos probados fue con un vino Merlot. El número de moscas capturadas con mezclas de vino / vinagre también variaron un poco según el tipo de vinagre, con el vinagre de arroz el mejor en capturar moscas entre los vinegares probados. El número de moscas capturadas varió poco con la edad del cebo, de 0 a 7 días de edad. Estos resultados ayudarán a los esfuerzos por mejorar el poder de los cebos utilizados para atrapar la mosca drosófila de alas manchadas, y proveer orientación para el aislamiento e identificación de atrayentes químicos en los vinos y vinegares.

The spotted wing drosophila (SWD), *Drosophila suzukii* (Matsumura) is native to Asia (Delfinado and Hardy 1977; Hauser 2011). It was introduced into North America by 2008, is now widespread in the eastern and western USA, as well as southern British Columbia, Canada (Hauser 2011), and is recently known in Europe (Calabria et al. 2010). It is of great concern as a pest of soft fruits, and is noteworthy as a *Drosophila* species in its ability to oviposit into maturing and undamaged fruits

(Kaneshiro 1983; Mitsui et al. 2006; Steck et al. 2009; Lee et al. 2011a). In the western USA, it has become a significant threat to berries, grapes, and cherries (Walsh et al. 2011; Beers et al. 2011; Lee et al. 2011b).

Traps baited with a variety of fermented food materials can be used to trap species of *Drosophila* (Kanzawa 1934; Hutner et al. 1937; Reed 1938; West 1961; Momma 1965; Birmingham et al. 2011; Landolt et al. 2011). Wines and

vinegars are used in trapping programs in USA and Canada to detect the presence of SWD, to assess the changing distribution of SWD, and to gain information about fly presence and density as a threat to crops (Steck et al. 2009; Walsh 2009; Beers et al. 2010). There are many materials suggested as baits for luring and trapping SWD, including vinegars and wines (Kanzawa 1934; Steck et al. 2009; Beers et al. 2010, 2011; Walsh et al. 2011). In a previous study (Landolt et al. 2011), we demonstrated SWD attraction to wine, vinegar, ethanol, and acetic acid. That same study showed that ethanol and acetic acid are co-attractive, as are wine and vinegar, in that more flies were trapped using mixtures of the two chemicals or the two food materials, respectively, rather than only 1 chemical or material. However the combination of wine and vinegar was much more attractive to SWD than the combination of ethanol and acetic acid. Those findings suggested a potential to isolate and identify chemical attractants from the mixture of wine and vinegar, in addition to ethanol and acetic acid, but did not indicate whether additional attractants from the mixture are emitted from the wine, the vinegar or both materials. Perhaps the identifications of these attractive chemicals might provide a useful synthetic chemical lure for trapping SWD.

We report here studies that build on our previous investigation of SWD attraction to wines and vinegars (Landolt et al. 2011), principally by determining respective roles of vinegar odor chemistry and wine odor chemistry, in addition to acetic acid and ethanol respectively, as contributors to the superior SWD attraction to a wine/vinegar mixture (Landolt et al. (2011). In addition, we assessed the importance of wine type, vinegar type, and bait age for bait attractiveness.

MATERIALS AND METHODS

The dome trap (Trappitt trap, Agrisense Ltd., Pontypridd, UK) was used in all experiments. Landolt et al. (2011) showed the efficacy of this trap design for ease of baiting with liquids and for capture of attracted SWD. This trap is yellow on the bottom 1/3 and clear on the top 2/3, with a 5-cm wide bottom entry for attracted insects. The invaginated trap bottom holds a drowning

solution or liquid bait. To facilitate the capture of flies entering traps and prevent decomposition of trapped insects, we added unscented dishwashing detergent (Palmolive Clear and Clean Spring Fresh Dishwashing Soap, Colgate-Palmolive Company, New York, New York, USA) and boric acid (Fisher Scientific, Santa Clara, California, USA) respectively to all baits. Borax prevents decomposition of captured insects in fermentation baits (Lopez & Hernandez-Becerill 1967; Shaw et al. 1970). For experimental baits, soap and boric acid were added in amounts needed to achieve the same concentrations as in the controls. These solutions were made in batches as 165 µL soap plus 40 g boric acid per 4 liters of water or bait. A dose of 300 mL of the drowning solution or bait was added to each trap. A randomized complete block design was used for all experiments. Unless otherwise stated, insects were removed from traps, traps and baits were replaced, and treatment positions randomized weekly. Unless otherwise stated, the wine used was Carlo Rossi Reserve Merlot (Carlo Rossi Vineyards, Fresno, California, USA) with 12% ethanol and the vinegar used was Safeway Apple Cider Vinegar (Safeway Inc., Pleasanton, California, USA) with 5% acidity.

Trapping experiments were conducted in Marion County, Oregon, in areas of commercial berry crops and abundant wild blackberry. Traps were placed 1.5 m high on vegetation, and were 10 m apart, with linear sets of traps (as experimental blocks) either along roadways or outside of field borders. Experimental blocks were > 50 m apart.

Experiment 1. Comparison of Vinegar plus Wine versus Acetic Acid plus Ethanol

This experiment tested the hypotheses that chemicals in wine in addition to ethanol enhance SWD attraction to a bait possessing wine, and that chemicals in vinegar in addition to acetic acid enhance SWD attraction to a bait possessing vinegar. Treatments (Table 1) were 1) 2% acetic acid in water, 2) 60% wine plus 2% acetic acid in water, 3) 7.2% ethanol plus 2% acetic acid in water, 4) 7.2% ethanol in water, 5) 7.2% ethanol plus 40% vinegar in water, and 6) 60% wine plus 40% vinegar. Baits for the 6 treatments were made up as 4 L- batches as shown in Table 1. Ten replicate

TABLE 1. AMOUNTS OF INGREDIENTS USED IN PREPARING 4-LITER BATCHES OF BAITS FOR TREATMENTS IN EXPERIMENT 1.

Treatment	acetic acid	ethanol	vinegar	wine	boric acid	dish soap
AA	80 mL	0 mL	0 mL	0 mL	40 g	12.5 µL
wine + AA	80 mL	0 mL	0 mL	2400 mL	40 g	12.5 µL
Etoh + AA	80 mL	300 mL	0 mL	0 mL	40 g	12.5 µL
Etoh	0 mL	300 mL	0 mL	0 mL	40 g	12.5 µL
Etoh + vinegar	0 mL	300 mL	1600 mL	0 mL	40 g	12.5 µL
wine + vinegar	0 mL	0 mL	1600 mL	2400 mL	40 g	12.5 µL

AA is acetic acid, and Etoh is ethanol.

blocks of this experiment were set up on 9 Mar and were maintained until 5 Apr 2011.

Experiment 2. Comparison of Wine Types as Mixed with Vinegar

This experiment tested the hypothesis that wine types vary in their attractiveness to SWD, when added to Safeway apple cider vinegar as a trap bait. The trap baits were 1) 40% vinegar in water, 2) 40% vinegar plus 60% blackberry wine (Pasck Cellars, Mount Vernon, Washington, USA), 3) 40% vinegar plus 60% raspberry wine (Hoodsport Winery, Hoodsport, Washington, USA), 4) 40% vinegar plus 60% of a white grape wine (Carlo Rossi Reserve Chardonnay, Carlo Rossi Vineyards, Modesto, California, USA), and 5) 40% vinegar plus 60% of a red grape wine (Carlo Rossi Reserve Merlot). The white grape wine contained 11% ethanol, while all other wines were 12% ethanol. The control was a 40:60 mixture of vinegar and water. Ten replicate blocks were set up on 8 Jun and were maintained until 10 Aug 2011.

Experiment 3. Comparison of Vinegar Types as Mixed with Merlot Wine

This experiment tested the hypothesis that vinegar types vary in their attractiveness to SWD, when added to the red grape wine as a trap bait. The trap baits were 1) 60% wine in water, 2) 60% wine plus 40% rice vinegar (Safeway® Select Rice Vinegar, Safeway Inc., Pleasanton, California), 3) 60% wine plus 40% Safeway apple cider vinegar, 4) 60% wine plus 40% white wine vinegar (Star Italian White Wine Vinegar, Star Fine Foods, Fresno, California, USA), and 5) 60% wine plus 40% red wine vinegar (Star Italian Red Wine Vinegar, Star Fine Foods, Fresno, California). Ten replicate blocks were set up on 10 Aug and were maintained until 1 Sep 2011. The rice vinegar as purchased was 4% acidity, and all other vinegars as purchased were 5% acidity.

Experiment 4. Effect of Bait Age on Attraction of Spotted Wing *Drosophila*

All traps were baited with a 40:60 mixture of Safeway Select Rice Vinegar and Carlo Rossi Re-

serve Merlot® wine. Batches of this mixture were set up in open polypropylene tubs (20 × 20 × 27 cm), to a depth of 11.5 cm. Tubers were held in a controlled environment room, at 23 °C and 10% RH, 7, 5, 3, and 1 d before baiting of traps in the field. Traps were baited and then checked after 24 h, providing the testing of baits that were 0, 1, 3, 5, and 7 d old. Ten block replicates of this experiment were conducted on 2 occasions, providing 20 replicates. Ten blocks of traps were set up on 21 Sep and maintained for 24 h, and ten blocks of traps were set up on 28 Sep 2011 and maintained for 24 h.

For each experiment, trap catch data were totaled for the duration of the test and square root transformed (Steel and Torrie 1960) before a 1-way ANOVA. Treatment means were separated by Tukey's Honestly Significant Difference Test, at $P = 0.05$ (DataMost 1995).

RESULTS

For each experiment, responses of male and female SWD flies to baits are summarized and presented by sexual gender in Tables 1-5.

Experiment 1. Comparison of Combinations of Wine, Vinegar, Ethanol, and Acetic acid

Numbers of flies captured in traps baited with acetic acid alone or ethanol alone were low (Table 2). Numbers of flies captured in traps baited with the combination of acetic acid plus ethanol were significantly greater than in traps baited with acetic acid alone or ethanol alone. Traps baited with acetic acid plus vinegar, ethanol plus vinegar, and wine plus vinegar captured similar numbers of flies, which were significantly greater than traps baited with acetic acid plus ethanol (Table 2). Totals of 1,335 female and 968 male SWD were captured in this experiment.

Experiment 2. Comparison of Wine Types, Each Mixed with Apple Cider Vinegar

Numbers of flies captured were significantly greater in traps baited with a mixture of vinegar plus wine, compared to vinegar alone, for all wine types tested (Table 3). Numbers of flies captured

TABLE 2. MEAN (\pm SEM) NUMBERS OF MALE AND FEMALE SPOTTED WING *DROSOPHILA* FLIES CAPTURED IN TRAPS BAITED WITH COMBINATIONS OF ACETIC ACID (AA), ETHANOL (ETOH), MERLOT WINE, AND APPLE CIDER VINEGAR (VIN).

	AA	AA + WINE	AA + ETOH	ETOH	ETOH + VIN	WINE + VIN
Female	0.7 \pm 0.5 c	32.7 \pm 14.4 a	14.1 \pm 10.1 b	0.2 \pm 0.1 c	31.9 \pm 12.9 a	28.1 \pm 11.3 a
Male	0.9 \pm 0.6 c	19.7 \pm 8.4 a	11.1 \pm 8.4 b	0.1 \pm 0.1 c	22.4 \pm 11.1 a	20.5 \pm 10.4 a

Means in a row followed by the same letter are not significantly different by Tukey's Honestly Significant Test at $P = 0.05$. For female trap catches, ANOVA $F = 5.61$, $df = 59$, $P < 0.001$. For male trap catches, ANOVA $F = 3.96$, $df = 59$, $P = 0.004$.

TABLE 3. MEAN (\pm SEM) NUMBERS OF MALE AND FEMALE SPOTTED WING DROSOPHILA FLIES CAPTURED IN TRAPS BAITED WITH APPLE CIDER VINEGAR ALONE (VIN) AND IN COMBINATION WITH RED GRAPE (RG), WHITE GRAPE (WG), RASPBERRY (RB) AND BLACKBERRY (BB) WINES.

	Vin	Vin + RG WINE	Vin + WG WINE	Vin + RB WINE	Vin + BB WINE
Female	4.4 \pm 0.7 d	27.2 \pm 4.7 a	17.5 \pm 2.3 bc	13.9 \pm 1.9 c	20.0 \pm 2.1 b
Male	4.2 \pm 0.9 c	25.7 \pm 4.7 a	16.4 \pm 2.9 b	17.2 \pm 2.2 b	19.1 \pm 3.8 b

Means in a row followed by the same letter are not significantly different by Tukey's Honestly Significant Test at $P = 0.05$. For female trap catches, ANOVA $F = 16.3$, $df = 49$, $P < 0.001$. For male trap catches, ANOVA $F = 8.8$, $df = 49$, $P < 0.001$.

were greatest in traps baited with vinegar plus red grape wine, and numbers of flies trapped were similar in traps baited with vinegar plus blackberry, raspberry, or white grape wines. Totals of 840 female and 843 male SWD were captured in this experiment.

Experiment 3. Comparison of Vinegar Types, Each Mixed with Merlot Wine

Numbers of male and female SWD were significantly greater in traps baited with a mixture of wine plus vinegar, compared to wine, for all vinegar types tested (Table 4). Numbers of SWD captured were greatest in traps baited with rice vinegar plus wine, and numbers of flies trapped were similar in traps baited with wine plus either apple cider vinegar, white wine vinegar, or red wine vinegar. Totals of 3,784 female and 5,716 male SWD were captured in this experiment.

Experiment 4. Effect of Bait Age on Attraction of SWD to a Mixture of Wine and Vinegar

There were no significant differences among captures of female or male SWD flies in traps baited with the wine/vinegar mixtures of different ages (Table 5). Totals of 550 female and 904 male SWD were captured in this experiment.

DISCUSSION

These results confirm prior demonstrations (Landolt et al. 2011) of attraction of both sexes of SWD to vinegar and to wine. Both vinegar and wine are suggested in extension web sites as baits for trapping SWD (Walsh 2009; Steck et al. 2009; Beers et al. 2010), and other species of *Drosophila* are attracted to vinegar (Becher et al. 2010);

hence the name vinegar fly for members of this genus. Our results also confirm the positive interaction between the vinegar and the wine as baits for SWD (Landolt 2011), which suggests that a combination of wine and vinegar may provide a bait that is superior in attractiveness, compared to vinegar alone or wine alone.

As reported before (Landolt et al. 2011), SWD flies were attracted to acetic acid in traps but were not attracted to ethanol. Acetic acid was tested because it is a major volatile chemical in vinegar (5% acidity in Safeway Apple Cider Vinegar) and is attractive to other species of *Drosophila* (Barrows 1907; Reed 1938; Dethier 1947; Becher et al. 2010). Ethanol was evaluated because it is a major volatile chemical in wine (12% in Carlo Rossi Reserve Merlot wine), and is also attractive to *Drosophila melanogaster* Meigen (Reed 1938). We have not shown attraction (by trap catch) of SWD to ethanol, although perhaps it might show a response to ethanol with a different ethanol dose or release rate. This study is the second demonstration of a positive interaction between acetic acid and ethanol as a bait or lure for SWD (after Landolt et al. 2011), which means that the combination of the 2 chemicals was more attractive than either chemical presented separately in traps. Barrows (1907) reported a positive interaction between acetic acid and ethanol for luring *Drosophila ampelophila* Loew in a laboratory olfactometer. Zhu et al. (2003), using a laboratory cage type assay, showed an orientation response of *D. melanogaster* to a blend of acetic acid, ethanol, and 2-phenylethanol. Other types of flies, such as Calliphoridae, are attracted to solutions of acetic acid plus ethanol (Dethier 1947).

The power of the acetic acid plus ethanol lure is quite weak in comparison to the attractiveness of the combination of vinegar and wine, which does

TABLE 4. MEAN (\pm SEM) NUMBERS OF MALE AND FEMALE SPOTTED WING DROSOPHILA FLIES CAPTURED IN TRAPS BAITED WITH MERLOT WINE ALONE AND IN COMBINATION WITH RICE VINEGAR (RV), APPLE CIDER VINEGAR (ACV), WHITE WINE VINEGAR (WWV), AND RED WINE VINEGAR (RWV).

	Wine	Wine + RV	Wine + ACV	Wine + WWV	Wine + RWV
Female	34.1 \pm 7.9 c	107.3 \pm 20.6 a	70.6 \pm 13.2 b	71.8 \pm 17.9 b	89.2 \pm 18.3 ab
Male	55.1 \pm 16.2 c	161.3 \pm 34.2 a	96.0 \pm 20.8 b	107.8 \pm 25.4 b	130.9 \pm 30.9 ab

Means in a row followed by the same letter are not significantly different by Tukey's Honestly Significant Test at $P = 0.05$. For female trap catches, ANOVA $F = 3.2$, $df = 49$, $P = 0.02$. For male trap catches, ANOVA $F = 2.5$, $df = 49$, $P = 0.05$.

TABLE 5. MEAN (\pm SEM) NUMBERS OF MALE AND FEMALE SPOTTED WING DROSOPHILA FLIES CAPTURED IN TRAPS BAITED WITH A MIXTURE OF MERLOT WINE AND APPLE CIDER VINEGAR, AGED FOR ZERO TO 7 DAYS BEFORE PLACEMENT IN THE FIELD FOR 24 HOURS.

	0 days	1 day	3 day	5 day	7 day
Female	3.8 \pm 1.7 a	4.9 \pm 2.1 a	6.1 \pm 2.0 a	5.8 \pm 1.9 a	6.1 \pm 2.2 a
Male	5.0 \pm 2.0 a	10.3 \pm 4.0 a	12.4 \pm 4.6 a	10.6 \pm 3.5 a	11.0 \pm 3.8 a

Means in a row followed by the same letter are not significantly different by Tukey's Honestly Significant Test at $P = 0.05$. For female trap catches, ANOVA $F = 0.56$, $df = 44$, $P = 0.69$. For male trap catches, ANOVA $F = 0.98$, $df = 59$, $P = 0.42$.

not support our earlier hypotheses that SWD attraction to vinegar is explained by their response to acetic acid and their attraction to wine is explained by their response to ethanol. SWD attraction to vinegar is greater than their response to acetic acid, their response to wine is greater than their response to ethanol, and their response to the combination of wine and vinegar is stronger than their response to the combination of acetic acid and ethanol. The greater response by SWD flies to vinegar compared to acetic acid suggests that additional chemicals in vinegar are attractive as well. Similarly, the attraction of SWD to wine and not to ethanol indicates that other compounds in wine are attractive to SWD.

It is interesting that numbers of SWD trapped were roughly equivalent for the combinations of vinegar plus wine, vinegar plus ethanol, and wine plus acetic acid. Two additional hypotheses might be considered in further studies to explore the fly behavior that provides this result. First, the attractive chemicals in vinegar and in wine may overlap partially or completely. For example, a number of ethyl esters and other compounds found by Blanch et al. (1992) in wine vinegar volatiles are reported by Qian et al. (2009) to be volatiles of Merlot wine, and Stökl et al. (2010) point out the occurrence of 2,3-butanediol acetate and acetoin acetate in both wine (Canas et al. 2008) and vinegar (Chinnici et al. 2009) headspace volatiles, as well as in the floral scent of a lily, *Arum palaestinum*, that is pollinated by Drosophilidae flies. A second hypothesis is that the fly response to volatiles from these baits may be redundant, with multiple chemicals eliciting the same behavioral response. The isolation and identification of attractive compounds from these materials should provide clarification of the nature of SWD attraction to these fermented food baits.

Vinegar plus wine might be used as a bait for SWD traps (Landolt et al. 2011), and it appears that a variety of types of vinegar, and a variety of types of wine, can suffice as part of this combination bait. All vinegars tested in combination with Merlot wine provided a significant increase in capture of SWD flies, and all wines tested in combination with apple cider vinegar provided a significant increase in captures also. Our results suggest that rice vinegar is more co-attractive with wine for SWD than the other vinegars test-

ed, and generally the Merlot wine was more co-attractive with vinegar than the other wines tested. However, there are brands and types of vinegar and very large numbers of wines produced that we did not test. So conclusions cannot be made regarding what might be a "best" vinegar or "best" wine as a component of a bait for SWD.

The lack of a significant variance in bait attractiveness to SWD with age (exposure time) was unexpected, because previous studies showed changes in the attractiveness of sweet baits to insects with the age of the bait. For example, the age of a molasses bait impacted the daily numbers of *Mocis latipes* Guenée grass looper moths captured over one wk (Landolt 1995), as did the age of a jaggery (palm sugar) bait for captures of the tobacco budworm moth *Heliothis virescens* (Fab.) (Landolt 1997). Under bait and field conditions conducive to microbial fermentation, attractive compounds might be generated in the bait during the period of aging or exposure, changing bait attractiveness with time. It was also considered that attractive volatiles in the bait might be evaporated and thus reduced or lost in the field over time, reducing the attractiveness of the bait. Our trap catch results do not support either hypothesis for the attractiveness of the mixture of wine and vinegar to SWD. The addition of boric acid to the bait to prevent decomposition of captured insects could also curtail bait fermentation, and presumably then the further generation of microbial metabolic byproducts. And perhaps the rate of evaporation of bait compounds that are attractive to SWD is too slow to have a significant effect over 7 d. Our results then do not indicate either a loss of attractive compounds over time from the bait or microbial generation of compounds, but rather a remarkable stability in attractiveness over the 7 d range of bait ages. Additional study over longer time periods, such as multiple wk, may be helpful to determine the stability of bait, if there is a need to minimize bait replacement and maximize bait longevity.

A useful synthetic chemical lure for SWD might be achieved from an analysis of the odor chemistry of these vinegars and wines, coupled with suitable bioassays, to identify the chemicals in these materials eliciting attraction. Results of each of these trapping tests provides some insight into the chemistry of SWD attraction to baits and

could help efforts to isolate and identify an attractive blend as a feeding attractant. It is assumed, based on the experimental results here and before (Landolt et al. 2011) that such a blend of compounds would include acetic acid combined with ethanol. The superiority of bait containing Merlot wine versus other wines, and rice vinegar versus other vinegars suggests that attractants might be more abundant in these products compared to the others tested. Alternatively, it is also possible that wines and vinegars vary in production of attraction agonists, although we have no evidence of this. The similar attractiveness of wine plus vinegar, wine plus acetic acid, and ethanol plus vinegar suggests either overlap in the wine and the vinegar attractant chemistry, or redundancy in SWD response to multiple compounds from these fermented food materials. We suggest that consideration of volatile chemicals produced by rice vinegar and Merlot wine might be pursued to isolate chemical attractants useful for trapping SWD.

These experiments were conducted over a range of conditions from spring into early autumn that might impact fly response to the bait. The temperatures occurring in the field during each experiment likely have effects on microbial activity, the rates of evaporation of volatiles from baits, and fly general activity levels. The population density of the fly certainly must change through the months of the field season, impacting the size of the potential pool of responders. And the relative availability of fruits of an appropriate stage of ripeness and decay will vary with the time of the season, and could impact fly hunger and responsiveness to bait, as well as provide competing odor cues. Comparisons cannot of course be made between the levels of fly response (numbers of flies captured) between experiments.

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