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Ecological effects of interplanted sweet alyssum and alfalfa in an organic day-neutral strawberry production system

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Production of day-neutral strawberries (*Fragaria x ananassa*) is increasing in the Upper Midwest region of the USA, resulting in an extended strawberry harvest season compared to traditional June-bearing production systems. However, the longer harvest season comes with additional insect pest pressure and the need for novel integrated pest management strategies. Spotted-wing drosophila (*Drosophila suzukii*; SWD) and tarnished plant bug (*Lygus lineolaris*; TPB) can decrease strawberry yield and fruit quality. Insecticides are the dominant management strategy for both insect pests; however, fewer effective insecticides are available in organic production systems. Interplanting is an integrated pest management strategy which can provide conservation biological control and may repel or attract species of interest through volatile organic compound (VOCs) emissions. We investigated the effect of interplanting alfalfa and sweet alyssum with day-neutral strawberry plants on fruit yield and quality, SWD infestation and TPB damage, arthropod abundance and diversity. Additionally, we measured the relative abundance of sweet alyssum VOCs, acetophenone and benzaldehyde, in the field because they may be aversive to SWD adults. The interplanting treatment inconsistently affected fruit production; in year one of the study, the control treatment had larger fruit than the other two treatments and, in year two, berries interplanted with sweet alyssum had more marketable yield than the other two treatments. Treatments did not affect SWD infestation or TPB damage. Acetophenone and benzaldehyde VOC production varied in the sweet alyssum plots by time of day and date. The control treatment had less arthropod abundance and diversity compared to the intercrop treatments. Intercropping may provide resources for arthropod communities but may not reduce key pest species such as SWD and TPB in day-neutral strawberries.

KEYWORDS

Drosophila suzukii, *Lygus lineolaris*, chemical ecology, biodiversity, integrated pest management, behavior modification, conservation biological control

1 Introduction

Strawberries are an economically important crop, popular globally for their nutritional content and flavor (Schwieterman et al., 2014; Petran et al., 2017). Research on extending the season and market for strawberries in the Upper Midwest region of the USA has focused on day-neutral strawberry (*Fragaria x ananassa*; DNS) production, which generates fruit later in the growing season, from mid-summer into fall compared to traditional June-bearing strawberry (JBS) cultivars (Petran et al., 2017; Anderson et al., 2019; Samtani et al., 2019). Although strawberry plants are host to many insect pests (Carroll et al., 2022), two key pests are particularly challenging for production of DNS in the Upper Midwest: tarnished plant bug (*Lygus lineolaris*; TPB) and spotted-wing drosophila (*Drosophila suzukii*; SWD), both of which are intensified by the extended growing season (Samtani et al., 2019).

SWD, a non-native vinegar fly, is highly polyphagous, feeding on a variety of fruit crop and non-crop hosts (Bellamy et al., 2013; Asplen et al., 2015; Lee et al., 2015; Little et al., 2020). Adult female SWD damage small and soft fruit (e.g., berries and stone fruit) during oviposition (Atallah et al., 2014). SWD ovipositors are sclerotized and enlarged compared to other drosophilids, which allows for oviposition during fruit ripening and egg or larvae infestation at the time of harvest (Atallah et al., 2014). Further reduction in fruit marketability is caused when SWD larvae feed on and develop within the mesocarp.

In the Upper Midwest, SWD populations peak between mid-August and mid-September which coincides with the peak harvest period of DNS (Anderson et al., 2019; University of Minnesota Extension, 2024). Most of the research conducted on SWD has focused on raspberry and blueberry crops, which have shown greater susceptibility to SWD infestations (Bellamy et al., 2013). In comparison, damage caused by SWD in strawberries has been described as relatively less severe, although recent studies report increased infestation (Goodhue et al., 2011; Ganjisaffar et al., 2023; Gullickson et al., 2024). Despite advances in cultural control techniques, management of SWD is still predominately managed with broad-spectrum chemical controls which have damaging ecological impacts on non-target species, soil, and water quality, and contribute to insecticide resistance (Biondi et al., 2012; Van Timmeren and Isaacs, 2013; Gress and Zalom, 2018; Van Timmeren et al., 2018; Gullickson et al., 2019; Sial et al., 2019; Schöneberg et al., 2020).

In addition to SWD, the native insect pest TPB causes substantial reduction in the quality and marketability of strawberries (Wold and Hutchison, 2003; Dumont and Provost, 2019, 2022; Hagler et al., 2020). TPB nymphs feed on strawberry blossoms with piercing-sucking mouthparts, which damages the flower receptacle leading to misshapen and unmarketable strawberry fruit. TPB is polyphagous, affecting cash crops such as cotton (Smith et al., 2023) and 130 other economically important plant species out of its 328 identified host plants (Young, 1986). Alfalfa (*Medicago sativa*) is considered one of its main host species (Esquivel and Mowery, 2007; Smith et al., 2023). While exclusion netting proves effective on a small scale, the primary management

approach for TPB relies on frequent insecticide applications or using tractor-mounted vacuums to remove nymphs from the field, both of which are broad spectrum, and vacuuming has not been consistently effective at reducing pest damage (Swezey et al., 2007; Chouinard et al., 2017; Lu et al., 2022). Only a limited number of organic chemical insecticides demonstrate efficacy against TPB. In organic settings, pyrethrin or azadirachtin-based insecticides are the most applied (Dumont and Provost, 2019). Moreover, TPB populations have developed resistance and antixenosis to various insecticide classes, necessitating the consideration of additional integrated pest management (IPM) tactics for small to medium-sized farms typical of the Upper Midwest (Smith et al., 2023).

Development of an effective push-pull pest management system for both insect pests could reduce insecticide risks to beneficial insects and be applicable in conventional and organic production systems (Khan et al., 2000; Cook et al., 2007). In DNS production, implementing border- and inter-plantings of attractive plant species could pull pests away from strawberry plants, while aversive plant species could push pests away from the host fruit (Hagler et al., 2020; Nieto et al., 2023; Hetherington et al., 2024). Plants and microbial yeast release volatile organic compounds (VOCs) that attract SWD to fruit crops, a behavior exploited for SWD monitoring with baited traps and attract-and-kill tactics (Cha et al., 2012; Keesey et al., 2015; Bueno et al., 2019). Recent studies have focused on aversive odorants to deter SWD from ovipositing in ripening fruit and for post-harvest protection (Renkema et al., 2016, 2017, 2020; Wallingford et al., 2016a; Bedini et al., 2020; Cha et al., 2020; Gullickson et al., 2020; Renkema and Smith, 2020; Stockton et al., 2021). Although various VOCs have reduced SWD fruit infestation in lab and field settings for raspberries, further optimization is needed due to unpleasant aromas for people (Wallingford et al., 2016a; Cha et al., 2020; Stockton et al., 2021), expense (Wallingford et al., 2016b; Kirkpatrick et al., 2018b), inadequate pest reduction due to no established acceptable threshold for SWD (Ganjisaffar et al., 2023), and lack of effective studies in day-neutral strawberry production systems (Renkema et al., 2020). Sweet alyssum (*Lobularia maritima*) has been shown to facilitate natural enemies and reduce other pests, and its two main floral VOCs, acetophenone and benzaldehyde, are deterrent to SWD in the laboratory (Begum et al., 2006; Hogg et al., 2011; Renkema and Smith, 2020; Tsuruda et al., 2022). Alfalfa has been investigated for its potential as an attractive sink for TPB in June bearing strawberries (Hetherington et al., 2024), but it remains uncertain if alfalfa would be effective throughout the longer DNS flowering season in the Upper Midwest. These plants also have the potential to provide beneficial insects with floral resources and thereby increase biodiversity (Hogg et al., 2011; Foti et al., 2017). However, the VOC composition of field-grown alfalfa and sweet alyssum, and their effect on pest damage to strawberries, remains unknown.

In this study, we investigated whether interplanting alfalfa and sweet alyssum with DNS plants affected: 1) fruit yield and quality; 2) SWD infestation and TPB damage; and 3) arthropod abundance and diversity. Additionally, we investigated the relative abundance of the acetophenone and benzaldehyde in field-grown sweet

allyssum flowers at different times throughout the day and the growing season. We hypothesized that yield and fruit quality would differ among interplanting treatments potentially lower due to competition for resources among the strawberries and interplants or insect pest pressure, or higher if the interplants provided resources for additional biological control or brought in pollinators. Additionally, we hypothesized that DNS interplanted with sweet allyssum would have lower rates of SWD infestation in strawberry fruit due to sweet allyssum flower volatiles, which would deter SWD females from ovipositing in fruit. In year two of our study, we investigated whether sweet allyssum produced deterrent VOCs in the field and the diurnal and seasonal timing of when they were produced. We also hypothesized that TPB populations and damage on strawberry fruit would be lower among the alfalfa treatment relative to the control, due to alfalfa attracting TPB away from the strawberry plants. Finally, we hypothesized that the arthropod communities would be more abundant and diverse in strawberries next to sweet allyssum and alfalfa because of additional plant diversity and floral resources compared to the control.

2 Materials and methods

2.1 Location and plant materials

This research was conducted at the Minnesota Agricultural Experiment Station on the University of Minnesota St. Paul campus on USDA certified organic land (45°0'31.09" N, 93°18'56.313" W) in 2021 and 2023. Composted manure was used as fertilizer prior to planting, followed with fertigation throughout the season (Neptune's Harvest Fish and Seaweed Fertilizer 2-3-1, Neptune's Harvest, Gloucester, MA) to supply the plants with 5.6 kg N ha⁻¹ week⁻¹. Bare root day-neutral strawberries (cv. Albion, Nourse Farms, Whately, MA) were planted on 17 May 2021 and 5 May 2023 on plastic mulch covered raised beds over drip irrigation. The two outer rows served as buffer rows to minimize edge effects, and the middle row was used for data collection ([Supplementary Figure 1](#)). The data row was a staggered double row with strawberry plants spaced 30.5 cm apart. Treatments consisted of transplanted seedlings for interplanted 1.5 m long sections of alfalfa (cv. Vernal, Johnny's Selected Seeds, Winslow, ME) or sweet allyssum (cv. Snow Crystals, Park Seed, Greenwood, SC) planted at 6.6 plants m⁻¹, compared to an unplanted control around the strawberry plants. Each treatment plot was replicated 4 times (12 plots total). Plots were spaced 10 m apart to minimize the potential for interference with the volatile treatments based on previous spotted wing drosophila chemical ecology research ([Wallingford et al., 2018](#)).

2.2 Strawberry production

All fully ripe strawberry fruit were harvested twice weekly from the data rows. Harvested fruits were placed in labeled plastic clamshells and stored in a cooler until they were brought to the

lab to record insect damage, yield (g), the number of fruits, and average fruit weight (g). In 2021, strawberries were harvested beginning on 21 June until 21 October. In 2023, strawberries were harvested from 19 June to 5 October. Harvest for each year concluded when freezing temperatures killed the remaining strawberry flowers.

2.3 Spotted-wing drosophila infestation and tarnished plant bug damage

Baited lures were not used for monitoring and assessing SWD populations in the strawberry plots, as these traps poorly reflect the number of SWD in the field and can bring in additional individuals through spillover ([Kirkpatrick et al., 2018a](#); [Leach et al., 2019](#)). A random subsample of 5 marketable fruits per treatment replication was used to determine SWD infestation (proportion of fruit with eggs and number of eggs per fruit) for each harvest date. Individual fruits were visually assessed under a dissecting microscope (8-35x magnification, Leica EZ4W) for SWD eggs as indicated by breathing filaments. Microscopy was used due to increased accuracy at quantifying SWD presence over salt water extraction methods, especially for eggs and first instar larvae ([Shaw et al., 2019](#); [Van Timmeren et al., 2021](#)).

TPB populations were sampled once per week throughout the flowering seasons (June – October). Between 10:00 and 14:00, five strawberry flower clusters were randomly selected for each treatment replication and were gently tapped above a white sheet of paper to count the combined number of TPB nymphs and adults. Plot sampling order was assigned randomly. TPB damage was assessed twice per week at harvest when marketable and unmarketable fruit was sorted. USDA number 1 or number 2 standards were used to determine whether fruit met marketability standards ([USDA-AMS, 2006](#)). Fruit was considered unmarketable due to TPB if more than approximately 10% of the fruit surface was deformed by TPB feeding.

2.4 Arthropod abundance and diversity

Arthropods in the strawberry plants were sampled weekly from 2 June to 12 October 2021 and every other week in 2023 from 8 June to 4 October. Arthropod specimens were collected using a handheld insect vacuum (Skil® 2810 18V vacuum, BioQuip) for a total of 2 minutes per treatment plot each week. The sampling order was assigned using randomly generated numbers in R. Vacuumed arthropod samples were stored in labeled cannisters that were taken to the lab and frozen at -20°C before pinning and subsequent identification based on morphological characteristics. Vacuumed arthropod samples were identified to a minimum of family level or the most specific taxonomic level when it was feasible to do so. Following identification, arthropods were categorized into functional feeding groups (detritivore/fungivore, herbivore, nectivore/pollinator, omnivore/other, and predator/parasitoid) based on available literature (i.e., [Hogg et al., 2011](#)).

2.5 VOC sampling and chemical analysis

To determine whether acetophenone and benzaldehyde were produced by sweet alyssum plants in the treatment plots and the timing of production, disposable research-grade, platinum-catalyzed polydimethylsiloxane (PDMS) discs (5 mm x 1 mm) (Interstate Specialty Products, Sutton, MA) were placed next to sweet alyssum flower clusters (approximately 30–40 individual flowers) to capture volatile organic compounds in the field. PDMS discs were washed and treated to remove absorbed compounds and were then attached to a paper clip and stored in a sealed glass jar until use (see: [Supplementary Material](#)). For each replication, three PDMS discs on paper clips were placed in 10 cm² Teflon bags (Welch Fluorocarbon Inc., Dover, NH) and bags were placed over flower clusters before sealing with a twist-tie. Sampling dates were 12 July, 23 August, and 14 September, all in 2023. Samples were collected starting at 6:00am, 11:00am, and 5:00pm, and each sampling period lasted for three hours. In each sweet alyssum treatment plot, two separate Teflon sampling bags with a set of three PDMS discs each were placed around flower clusters. At each sampling period, two Teflon sampling bags with three PDMS discs each were also placed in the field, but not around flowers, as negative controls. After three hours, bags were removed from the flower clusters, re-sealed, and placed on dry ice while transporting from the field to the lab. PDMS discs were removed from the paper clip and placed in an amber glass vial along with 150 μ L 50:50 dichloromethane:ethyl acetate solvent to extract absorbed compounds. The vials were placed on ice and gently shaken for 1 hour. The extraction solvent was transferred into glass inserts in autosampler vials and the contents were analyzed with gas chromatography-mass spectrometry (GC-MS). GC-MS analysis was performed using an Agilent 7890A GC and 5973 mass selective detector (MSD) single quadrupole instrument with a Gerstel MPS 2 autosampler. Helium was used as the GC carrier gas with a 7.5 min solvent delay. The flow rate was held constant at 1 mL/min. Samples (1 μ L) were injected using a Gerstel Multipurpose sampler (MPS), in pulsed splitless mode to an Agilent 30m DB-5MS UI, 0.25 mm I.D., 0.25 μ m film thickness capillary GC column. Inlet and interface temperatures were set to 280°C. The initial oven temperature was 70°C and was held for 4 min. Oven temperature was then increased at a rate of 15°C/min to 270°C where it was held for 4 min before returning to initial settings. The quadrupole temperature was set to 150°C and the source temp: 230°C. The MS scan range was 30–220 *m/z*.

2.6 Statistical analysis

Strawberry production data, i.e., cumulative total and marketable yields (g/plant), were first assessed for normality using the Shapiro-Wilk test and visual inspection of histograms and quantile-quantile plots. Separate non-parametric Kruskal-Wallis tests were initially used to assess the effects of treatment and year on these yields. Data were not pooled because a significant year effect was observed. Instead, each year was analyzed independently

for treatment effects. Within-year data satisfied the requirements for a one-way ANOVA, for which yield was the response variable and treatment was the explanatory variable. Tukey's test was used for *post-hoc* analyses.

A one-way ANOVA test was used to analyze the mean number of SWD eggs per strawberry for each year independently after significant differences were observed between years, preventing data from being pooled. For the proportion of infested strawberries, only the 2023 data met the necessary requirements, and in that case one-way ANOVA was used to determine treatment effects within each year, otherwise Kruskal-Wallis was used. TPB scouting data were integer counts and were analyzed using a generalized linear model (GLM) with a negative binomial distribution. The TPB count was the response variable, and treatment, year, and a treatment-by-year interaction were included as explanatory variables. The proportion of TPB-damaged fruit at the end of the season was analyzed with a two-way ANOVA to assess the effects of treatment and year.

To analyze arthropod family composition, family count data from each treatment and sampling date were square-root transformed to reduce the influence of highly abundant families. A non-metric multidimensional scaling (NMDS) was used for visualization, with the NMDS performed on a Bray-Curtis dissimilarity matrix. A permutational multivariate analysis of variance (PERMANOVA), with 9,999 permutations, was used to test differences in community composition among treatments, years, and a treatment year interaction. To analyze whether there were any differences in specific functional groups or individual families of interest, generalized linear models with a Poisson distribution followed by a one-way ANOVA were used.

GC-MS data were analyzed using ChemStation (Agilent) and MZmine (v2.53; [Pluskal et al., 2010](#)). Benzaldehyde and acetophenone peaks were identified by comparison of fragmentation patterns with those from the NIST 20 EI database using ChemStation and confirmed by co-injection of commercially obtained standard compounds (Sigma-Aldrich, Milwaukee, WI). Sample peak heights at the specified retention times were baseline corrected (GC-MS peak height of a treatment sample minus the peak height of a negative control) to reduce instrument noise and determine relative abundance of target molecules before statistical analysis. The abundance was relative to the negative control as well as to compare sampling times and dates. Separate Kruskal-Wallis tests were performed to assess the effects of time and date on the baseline corrected peak height of acetophenone and benzaldehyde, with the peak height of acetophenone or benzaldehyde as the response variable and time or date as explanatory variables.

3 Results

3.1 Strawberry production

Year had a significant effect on total yield, marketable yield, and the proportion of marketable fruit in this experiment ([Table 1](#); [Figure 1](#)). Cumulative total yield was significantly greater in 2021 than in 2023 (Kruskal-Wallis; $X^2 = 10.453$, $df = 1$, $P = 0.001$).

TABLE 1 Strawberry production (total and marketable yield) among interplanting treatments in 2021 and 2023.

Treatment	Total yield [mean $\pm$ SE (g/ plant)]	Marketable yield [mean $\pm$ SE (g/ plant)]
2021		
Alfalfa	404.15 $\pm$ 53.29	302.35 $\pm$ 45.04
Sweet alyssum	430.56 $\pm$ 32.89	313.42 $\pm$ 33.83
Control	529.24 $\pm$ 53.53	413.42 $\pm$ 34.10
	P = 0.2019	P = 0.1301
2023		
Alfalfa	317.64 $\pm$ 25.80	152.07 $\pm$ 20.10 a*
Sweet alyssum	336.32 $\pm$ 28.01	204.00 $\pm$ 7.76 b
Control	298.35 $\pm$ 16.02	146.31 $\pm$ 10.81 a
	P = 0.5527	P = 0.0313

*Letters denote statistically significant differences within columns within years by Tukey's *post hoc* test at $P < 0.05$.

Cumulative marketable yield was also significantly greater in 2021 compared to 2023 (Kruskal-Wallis; $X^2 = 15.87$, $df = 1$, $P < 0.001$).

In 2021, there were no significant differences in the cumulative total yield (ANOVA; $F = 1.922$, $df = 2, 9$, $P = 0.2019$), cumulative marketable yield (ANOVA; $F = 2.58$, $df = 2, 9$, $P = 0.130$) among the three treatments (Table 1, Figure 1). In 2023, cumulative total yield (ANOVA; $F = 0.6337$, $df = 2, 9$, $P = 0.5527$) was not different among

treatments. However, cumulative marketable yield was significantly different among the three treatments (ANOVA; $F = 5.214$, $df = 2, 9$, $P = 0.0313$); with greater marketable yield in the sweet alyssum interplanted strawberries compared to the alfalfa interplanted or control treatments.

3.2 Spotted-wing drosophila fruit infestation and tarnished plant bug damage

The average number of SWD eggs per strawberry during the peak of the harvest season (1 Aug to end of season, 21 Oct 2021 and 5 Oct 2023) ranged from 0.40 to 1.04 (Table 2). The number of eggs per strawberry was significantly lower in 2021 compared to the 2023 growing season (ANOVA; $F = 6.986$, $df = 1, 18$, $P = 0.0167$). There were no significant differences in the number of SWD eggs in strawberries among the three treatments in either year (ANOVA; 2021: $F = 1.488$, $df = 2, 9$, $P = 0.276$; 2023: $F = 1.624$, $df = 2, 9$, $P = 0.250$).

There were significant differences between years in the proportion of SWD infested strawberries (Kruskal-Wallis; $X^2 = 4.083$, $df = 1$, $P = 0.043$), with a greater proportion of strawberries infested in 2023 compared to 2021. However, among treatments, no significant differences in the proportion of SWD infested strawberries were observed in either year (ANOVA; 2021: $F = 0.763$, $df = 2, 9$, $P = 0.494$; 2023: $X^2 = 0.5$, $df = 2$, $P = 0.779$) (Table 2).

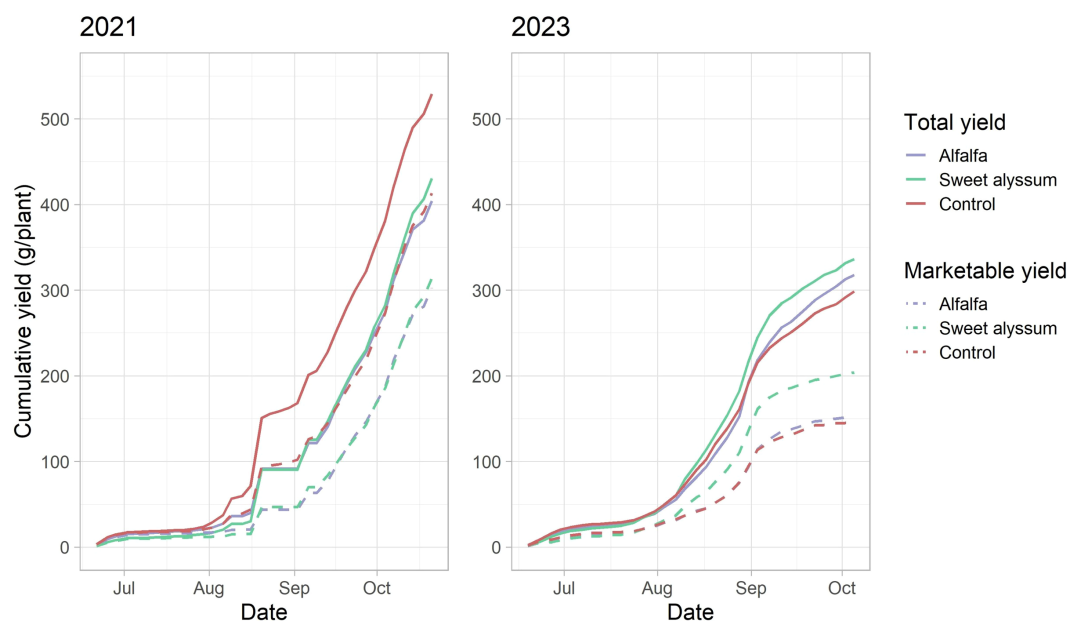


FIGURE 1

The cumulative total yield (g / plant) (solid lines) and marketable yield (g / plant) (dashed lines) of day-neutral strawberries (*Fragaria x ananassa* cv. Albion) when grown with two interplanting treatments and a control without an interplant in St. Paul, Minnesota, U.S.A. Both yield measurements were significantly lower in 2023 compared to 2021 (total yield, $p < 0.001$; marketable yield, $p < 0.001$). In 2023, the strawberry plants interplanted with sweet alyssum had significantly greater marketable yield (g / plant) than the alfalfa interplanted treatment or control ($p = 0.031$).

TABLE 2 *Drosophila suzukii* (SWD) infestation (number of eggs per berry and proportion of infested berries) in day-neutral strawberries among interplanting treatments in 2021 and 2023.

	SWD eggs [mean $\pm$ SE (No. eggs/berry)]	Proportion of infested berries [mean $\pm$ SE]
Treatment	2021	
Alfalfa	1.03 $\pm$ 0.23	0.14 $\pm$ 0.02
Sweet alyssum	0.99 $\pm$ 0.22	0.17 $\pm$ 0.02
Control	0.68 $\pm$ 0.16	0.13 $\pm$ 0.02
	P = 0.276	P = 0.494
	2023	
Alfalfa	0.40 $\pm$ 0.10	0.17 $\pm$ 0.03
Sweet alyssum	0.76 $\pm$ 0.14	0.21 $\pm$ 0.03
Control	0.56 $\pm$ 0.11	0.22 $\pm$ 0.03
	P = 0.250	P = 0.7788

Data is from 1 August through the end of the season in both years to correspond with bulk of the harvest and due to minimal SWD infestation prior to that time.

The average weekly tarnished plant bug nymph counts ranged from 1.47 to 2.36 and were not significantly different among the three treatments in either year (Table 3). Likewise, the proportion of unmarketable fruit due to TPB feeding was not significantly different among the three treatments (Table 3). TPB counts were significantly lower in 2023 than in 2021 (GLM; $X^2 = 13.774$, $P = 0.0002$), but the proportion of unmarketable fruit was not significantly different between years (GLM; $X^2 = 2.692$, $P = 0.101$).

TABLE 3 Tarnished plant bug (*Lygus lineolaris*; TPB) counts and damage on day-neutral strawberries among interplanting treatments in 2021 and 2023.

	TPB counts [mean $\pm$ SE (No. nymphs)]	Proportion of unmarketable fruit [mean $\pm$ SE]
Treatment	2021	
Alfalfa	2.36 $\pm$ 0.19	0.32 $\pm$ 0.03
Sweet alyssum	2.05 $\pm$ 0.21	0.33 $\pm$ 0.03
Control	2.36 $\pm$ 0.25	0.25 $\pm$ 0.02
	P = 0.481	P = 0.637
	2023	
Alfalfa	1.64 $\pm$ 0.23	0.28 $\pm$ 0.02
Sweet alyssum	1.47 $\pm$ 0.24	0.21 $\pm$ 0.02
Control	1.61 $\pm$ 0.24	0.26 $\pm$ 0.02
	P = 0.875	P = 0.283

TPB counts are the number of nymphs dislodged from 5 haphazardly selected flower clusters. TPB damage is reported as the proportion of unmarketable fruit due to TPB feeding.

3.3 Arthropod abundance and diversity

The number of sampled arthropod specimens totaled 5949 and was made up of 15 orders (Table 4) and 99 families (Supplementary Table 1). Arthropod family composition was significantly influenced by treatment (PERMANOVA; pseudo-F=1.55, $df = 2$, 319, $P = 0.036$) and year (PERMANOVA; pseudo-F=18.67, $df = 1$, 319, $P < 0.001$). However, there was no significant interaction between treatment and year (PERMANOVA; pseudo-F=0.46, $df = 2$, 319, $P = 0.989$), suggesting that the effect of treatment on family composition was consistent between the two years. Pairwise comparisons showed a significant difference in family composition between the control and sweet alyssum treatments (pairwise PERMANOVA; pseudo-F=1.72, $df = 1$, 212, $P = 0.049$). No significant differences were found between the alfalfa and control plots (pairwise PERMANOVA; pseudo-F=1.14, $df = 1$, 215, $P = 0.315$) and only marginal differences between the alfalfa and sweet alyssum plots (pairwise PERMANOVA; pseudo-F=1.55, $df = 1$, 217, $P = 0.089$).

The composition of arthropod functional groups (Table 5) was significantly affected by year (PERMANOVA; pseudo-F=20.79, $df = 1$, 309, $P < 0.001$). However, the effect of treatment (PERMANOVA; pseudo-F=1.35, $df = 2$, 309, $P = 0.233$) and the interaction between treatment and year (PERMANOVA; pseudo-F=0.43, $df = 2$, 309, $P = 0.864$) were not significant. The control treatment had significantly fewer herbivores compared to the sweet alyssum or alfalfa treatments in 2021, even after accounting for sampling date, but no differences were observed in 2023 (GLM; 2021: $X^2 = 6.539$, $df = 2$, $P = 0.038$; 2023: $X^2 = 3.433$, $df = 2$, $P = 0.180$). Additionally, there were significantly fewer predators and parasitoids in the control compared to the other two treatments in 2021, and marginally fewer in 2023 (GLM; 2021: $X^2 = 6.748$, $df = 2$, $P = 0.034$; 2023: $X^2 = 5.921$, $df = 2$, $P = 0.052$). However, there were no significant differences in the number of nectivores and pollinators among the treatments (GLM; 2021: $X^2 = 0.9003$, $df = 2$, $P = 0.638$; 2023: $X^2 = 0.108$, $df = 2$, $P = 0.947$).

Although there were numerical differences, the number of individual specimens collected from treatment groups of specific families of interest did not vary significantly among the three treatments in either year. There were no significant differences among treatments for the pest families of interest Drosophilidae (e.g., SWD) (GLM; $X^2 = 1.5458$, $df = 2$, $P = 0.4617$; 2023: $X^2 = 0.511$, $df = 2$, $P = 0.774$), and Miridae (e.g., TPB) (GLM; $X^2 = 2.9152$, $df = 2$, $P = 0.2328$; 2023: $X^2 = 0.729$, $df = 2$, $P = 0.694$). There were also no significant differences for beneficial generalist predators Anthocoridae (e.g., minute pirate bug, *Orius insidiosus*) (GLM; $X^2 = 3.0595$, $df = 2$, $P = 0.2166$; 2023: $X^2 = 1.516$, $df = 2$, $P = 0.469$), or Nabidae (e.g., *Nabis americanus*) (GLM; 2021: $X^2 = 0.20683$, $df = 2$, $P = 0.9018$; 2023: $X^2 = 0.2258$, $df = 2$, $P = 0.8932$).

3.4 VOC sampling and chemical analysis

Relative abundances of acetophenone ($X^2 = 4.826$, $df = 1$, $P = 0.028$) and benzaldehyde ($X^2 = 4.264$, $df = 1$, $P = 0.039$) were

TABLE 4 Number of arthropod specimens identified to order level^a collected from day-neutral strawberry plants among interplanting treatment during vacuum sampling in 2021 and 2023.

Arthropod order	Treatment			Totals ^b
	Alfalfa	Sweet alyssum	Control	
Acari	8	8	3	19
Araneae	91	83	82	256
Coleoptera	120	142	107	369
Collembola	101	108	90	299
Diptera	506	556	381	1443
Hemiptera	1011	859	785	2655
Hymenoptera	188	201	160	549
Lepidoptera	5	24	8	37
Neuroptera	3	4	6	13
Opiliones	21	26	19	66
Orthoptera	1	4	4	9
Psocodea	3	6	1	10
Thysanoptera	0	1	2	3
Unknown	81	67	68	216
Grand Total	2139	2089	1721	5949

^aPlease see [Supplementary Table 1](#) for counts of arthropod specimens identified to family level with their functional groups.

^bNumbers in bold refer to the total across treatments (for rows) and total within treatments (for columns).

significantly greater in sweet alyssum treatments compared to the negative controls. There were significantly different relative abundances of acetophenone among the three sampling times during the day ($X^2 = 11.303$, $df = 2$, $P = 0.004$). There was a

TABLE 5 Count of arthropod specimens collected from day-neutral strawberry plants among interplanting treatment during vacuum sampling in 2021 and 2023 and categorized in functional groups^a.

Functional group	Treatment			Totals ^b
	Alfalfa	Sweet alyssum	Control	
Detritvore/fungivore	414	423	332	1169
Herbivore	1011	990	820	2821
Nectivore/pollinator	43	60	52	155
Omnivore/other	140	118	128	386
Predator/parasitoid	519	485	378	1382
Grand Total	2127	2076	1710	5913

^aArthropods were categorized into functional feeding groups (detritvore/fungivore, herbivore, nectivore/pollinator, omnivore/other, and predator/parasitoid) based on available literature (i.e., [Hogg et al., 2011](#)).

^bNumbers in bold refer to the total across treatments (for rows) and total within treatments (for columns).

significantly lower abundance of acetophenone during the evening sampling time ([Figure 2A](#)). Likewise, benzaldehyde relative abundances were significantly different among the three sampling times during ($X^2 = 16.802$, $df = 2$, $P = 0.0002$). All three time periods were significantly different from each other. Additionally, there were significant differences in relative abundances for both acetophenone ($X^2 = 36.225$, $df = 2$, $P < 0.0001$) and benzaldehyde ($X^2 = 21.505$, $df = 2$, $P < 0.0001$) among the three sampling dates. For acetophenone, relative abundance was significantly lower on 23 Aug compared to the two other dates ([Figure 2B](#)). Benzaldehyde relative abundance was significantly greater on 12 Jul compared to the two other dates.

4 Discussion

This study investigated the effect of interplanting sweet alyssum and alfalfa on fruit production and insect pest management in day-neutral strawberries. The effect of interplanting treatments on day-neutral strawberry production was variable between the two years of this study; the treatments affected marketable yield in 2023, but did not affect total yield, nor the number of berries produced in either year. The sweet alyssum treatment had greater marketable yield than the other treatments in 2023. We did not observe more pollinators or fewer herbivores in the sweet alyssum compared to the control.

Year affected total and marketable yields, potentially due to seasonal environmental differences. For example, the 2023 growing season ended approximately two weeks earlier than the 2021 season. Another explanation for lower yields in the second year of this study could have been due to fungal pathogens. Although no strawberries were planted in the plot in 2022, strawberry fungal pathogens such as verticillium wilt (*Verticillium* sp.) may have persisted in the soil and contributed to reduced yields in the second year of the study ([Anderson et al., 2019](#)).

Treatments did not affect SWD oviposition or TPB counts in the DNS. For SWD, treatments did not affect egg counts nor the proportion of infested fruit in either year of this study. This is consistent with another study with JBS, in which [Tsuruda et al. \(2022\)](#) concluded that interplanting sweet alyssum alongside JBS plants did not decrease SWD infestation. The authors suggested that sweet alyssum may be more effective for fruit crops which ripen later in the season because it may support late season parasitoid adults as they establish a local population ([Tsuruda et al., 2022](#)). However, we did not observe any effect on SWD with a comparatively late season strawberry harvest. Another study with peppermint interplants found a similar lack of treatment effect in the field, although laboratory results were promising ([Renkema et al., 2020](#)). Likewise, TPB counts and impact on strawberries was not affected by treatment. Although other studies have found that alfalfa is the preferred host of TPB and perimeter strips functioned as a sink for TPB, we found no evidence of this effect in day-neutral strawberries ([Esquivel and Mowery, 2007](#); [Hetherington et al., 2024](#)). [Hetherington et al. \(2024\)](#) suggest spatial separation and a short period of JBS susceptibility would be necessary for alfalfa to

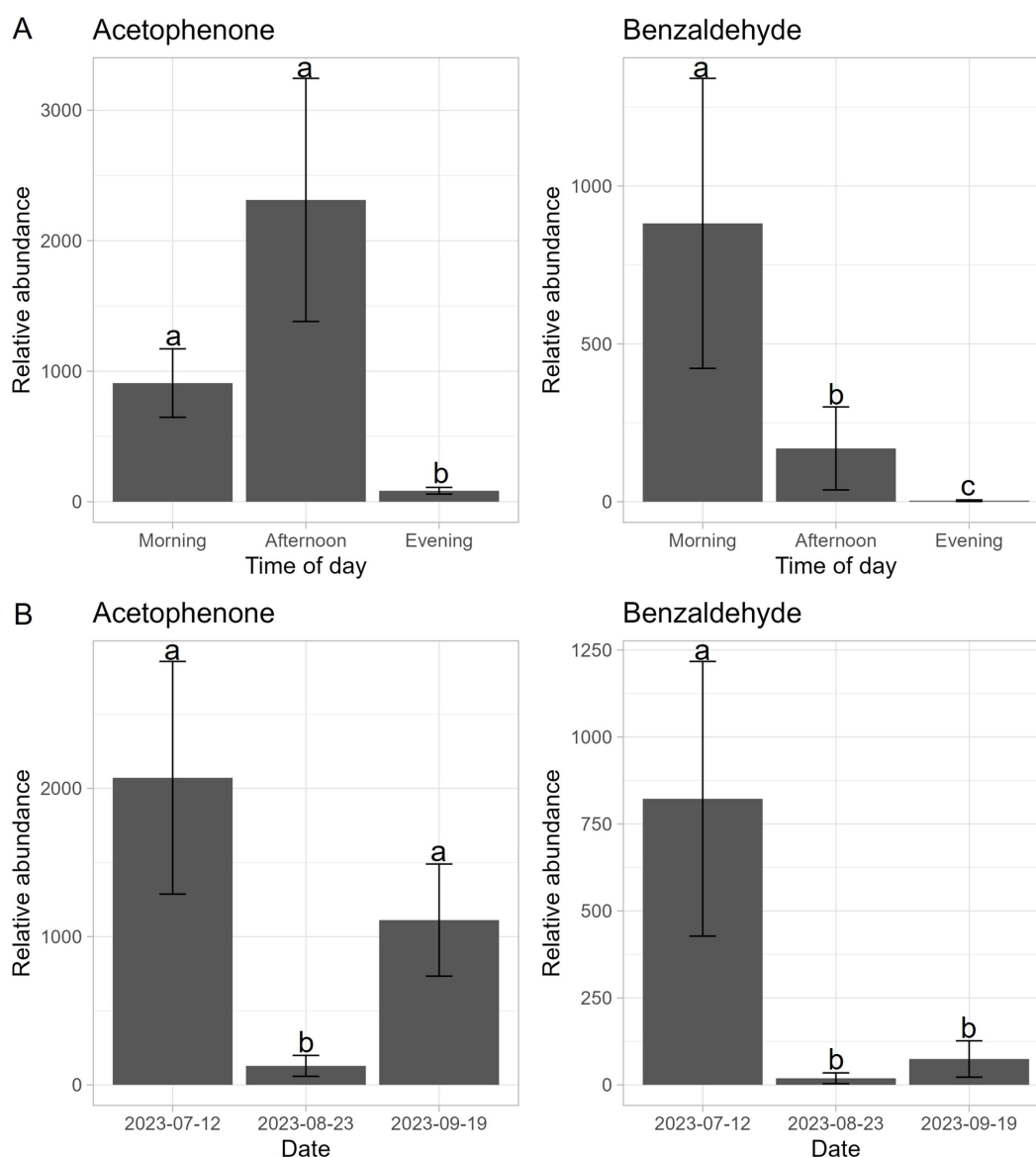


FIGURE 2

Relative abundances (sample peak height of treatment minus the negative control) of acetophenone and benzaldehyde produced by sweet alyssum (*Lobularia maritima*) at three different (A) time periods, morning (6:00 am - 9:00 am), afternoon (11:00 am - 2:00 pm), and evening (5:00 pm - 8:00 pm) and (B) separate dates, 12 July, 23 August, and 19 September 2023 in St. Paul, Minnesota. Letters denote significant differences among time periods for each molecule at $\alpha=0.05$.

act as a net sink, rather than both a sink and source. We conclude that alfalfa is likely not a suitable trap crop for TPB in small-scale day-neutral strawberry production, since TPB can still move from alfalfa into strawberry fields even with some spatial separation.

To understand how sweet alyssum may function as a source of repellent or attractive volatile organic compounds, we collected and analyzed the two main VOCs, acetophenone and benzaldehyde, from the flowers at three different time points on three different days in 2023. Previous studies identified acetophenone and benzaldehyde as main compounds of sweet alyssum flower aroma and that they showed some repellency towards SWD, although benzaldehyde showed no effect on SWD in another study (Wallingford et al., 2016b; Renkema and Smith, 2020). Our study

focused on these likely repellent compounds; however, vegetative tissue or trace floral VOCs may have also changed the arthropod communities and behavior. We observed inconsistent production of these SWD repellent compounds in the field, which could explain why other studies have not found them to be successful at limiting SWD infestation either. Compounds peaked in the morning (benzaldehyde) and afternoon (acetophenone) and were negligible in the evening. Since SWD has crepuscular behavior (Jaffe and Guédot, 2019), and sweet alyssum appears to produce the most aroma during mid-day, it follows that there may be some temporal incompatibilities of using repellent intercrops in a push-pull setting. Future studies investigating push-pull scenarios with living repellent plants should consider the concentration and timing of

VOC production and not assume that it is constant. It is possible that these volatile compounds are produced earlier in the day to correspond to when diurnal pollinators are most active (Hoballah et al., 2005; Fenske and Imaizumi, 2016). Additionally, relative abundance of these compounds was affected by sampling date. Some days (12 July and 19 September 2023) had high relative abundances and 23 August had low to no measurable abundance, even though there were no apparent differences in the number of flowers in each sampling bag, which further suggests that these treatments may only be effective some of the time. Therefore, although there are likely benefits of interplanting sweet alyssum to support arthropod biodiversity, it is unlikely to be a viable repellent for SWD due to the temporally inconsistent production of the volatiles.

Another objective of this study was to investigate whether the treatments provided a conservation biological control benefit by affecting arthropod abundance and diversity. In the treatments, we observed greater arthropod family diversity at specific sampling times and greater arthropod abundances both on a per sample basis and over the course of the season. Herbivores, predators, and parasitoids were all more abundant in the treatments compared to the control. We observed more predators and parasitoids in the treatments in both years, suggesting that alfalfa and sweet alyssum support beneficial insects from a conservation biological control standpoint. This is consistent with the findings from Lu et al. (2022), where the authors found that increased woody-habitat near the agroecosystem contributed to greater abundances of predators, however, they did not find differences in *Lygus* populations based on nearby habitat.

Increasing flowering plant diversity in agricultural ecosystems has the potential to support arthropod biodiversity, although beneficial functional groups were not the only ones affected by the treatments (Connelly et al., 2015; Lu et al., 2022). Treatments had more herbivores in 2021, which could have negative effects on strawberry production, although no differences were observed in 2023. Finally, there were no differences in the number of pollinators among the three treatments, so although these treatments increased flower resources and diversity, this likely did not result in more pollination services. Additionally, all treatments were receiving the same fertilizer so the reason for greater yields in the sweet alyssum treatment is unknown. DNS cultivar flowers are self-compatible, and will produce fruit in the absence of pollinators, but bee visits have been shown to increase fruit mass by 35 to 40% (Chagnon et al., 1993; Connelly et al., 2015). The number of individual specimens from specific families of interest did not vary among the treatments, adding to our previous evidence that sweet alyssum did not repel SWD, and alfalfa did not attract TBP. We also failed to observe more individuals from specific generalist predator families such as Anthocoridae and Nabidae. By contrast, a recent study in Minnesota apple found that Anthocoridae was the most abundant generalist predator (Nelson, 2023). For DNS, the effects of treatments appear to be general, and lack evidence for targeting specific taxa, potentially because the pests and some beneficial arthropods are polyphagous, and not specialists to DNS.

5 Conclusion

Interplanting day-neutral strawberries with sweet alyssum or alfalfa increased insect abundance and diversity, particularly for herbivore and predator, and parasitoid families, which may have positive implications for supporting arthropod biodiversity in agroecosystems. However, there was no observed SWD or TBP pest management benefit from these treatments and there were inconsistent effects on fruit production. More research is needed on using living plants to produce aversive and attractive volatiles *in situ* due to the complex nature of volatile quantity and timing.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

MG: Methodology, Writing – review & editing, Investigation, Conceptualization, Data curation, Formal analysis, Writing – original draft, Funding acquisition, Visualization. JS: Methodology, Data curation, Supervision, Investigation, Resources, Writing – review & editing. AH: Project administration, Visualization, Data curation, Methodology, Investigation, Conceptualization, Funding acquisition, Supervision, Writing – review & editing, Resources. MR: Writing – original draft, Resources, Funding acquisition, Project administration, Data curation, Conceptualization, Methodology, Supervision, Writing – review & editing, Investigation.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2025.1651123/full#supplementary-material>

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