



OPEN Season-dependent synergism between the male-attractive plant volatile benzaldehyde and the sex pheromone of the Oriental fruit moth, *Grapholita molesta*

Ajay P. Giri^{1,3}, Brent D. Short^{2,3} & Jaime C. Piñero^{1,3}✉

Herbivorous insects possess highly developed olfactory systems that enable them to detect, process, and respond to volatile cues emitted by host and nonhost plants. This study evaluated the field response of male and female Oriental fruit moths, *Grapholita molesta* (Lepidoptera: Tortricidae), to the aromatic plant volatile benzaldehyde (BEN). We evaluated BEN alone, in combination with the *G. molesta* sex pheromone, or with a four-component kairomonal lure (PHEROCON MEGALURE CM 4 K DUAL). Our findings demonstrate that (1) BEN alone is a male *G. molesta* attractant with efficacy comparable to that of Megalure or the sex pheromone; (2) the addition of BEN at low or medium doses to either Megalure or pheromone lures significantly increases the number of male captures; and (3) BEN interacts with the *G. molesta* pheromone in a season-dependent manner, exhibiting synergistic effects during the middle-season and additive effects in the early and late seasons. This discovery of seasonal synergism underscores benzaldehyde's unique role and highlights its potential to enhance pheromone-based lures without the need for additional host volatiles, providing a valuable tool for optimizing semiochemical-based monitoring and control strategies tailored to seasonal population dynamics.

Keywords Behavior, Monitoring, Semiochemical, IPM, Synergism, Sensory ecology

Insects rely on highly specialized olfactory systems to detect, process, and respond to chemical cues in their environment¹. Within Lepidoptera, semiochemicals, including host plant volatiles and sex pheromones, play pivotal roles in mediating insect behavior. This information is crucial to better understand the patterns of host plant use and for the development of more efficient monitoring and/or control tactics^{2–4}.

A major advancement in pest control is the implementation of mating disruption techniques, wherein synthetic sex pheromones are deployed at high densities to interfere with mate finding, thereby reducing reproductive success^{5–9}. Additionally, semiochemical-based attractants that target both male and female moths are being explored for their potential in integrated pest management (IPM) strategies, including attract-and-kill techniques¹⁰. Because the success of these approaches relies on a comprehensive understanding of insect olfactory responses and the complex interactions between semiochemicals¹¹, unremitting research is essential to refine existing systems and develop more effective strategies for pest management.

Research suggests that complex blends of host-plant-derived volatiles are often required to elicit significant attraction in tortricid moths^{12,13}. This phenomenon is particularly relevant for the Oriental fruit moth (OFM), *Grapholita molesta* (Busck), a significant pest of stone and pome fruits worldwide^{14–16}. Laboratory studies have demonstrated that a five-component blend of three green leaf volatiles and two aromatic compounds (benzaldehyde and benzonitrile) was as attractive to mated female *G. molesta*¹⁵ as the complete natural blend of peach shoot volatiles, which includes more than 20 compounds¹⁴. However, individual plant volatiles often exhibit weak attractiveness when presented alone^{12,14,17}. Understanding how some chemical compounds interact with sex pheromones may increase their utility in pest management programs. For example, combinations of plant volatiles and sex pheromones can enhance attraction in tortricid moths, as demonstrated by Varela et

¹Stockbridge School of Agriculture, University of Massachusetts, Amherst, MA 01003, USA. ²Trécé Inc, Hedgesville, WV 25427, USA. ³Ajay P. Giri, Brent D. Short and Jaime C. Piñero contributed equally to this work. ✉email: jpinero@umass.edu

al.¹⁸, who reported increased neurophysiological responses in male *G. molesta* when suboptimal doses of sex pheromones were added to a five-component volatile mixture.

While significant strides have been made in devising attractants and improved trapping systems for *G. molesta*, refinements are still needed, particularly when potential behavioral differences among pest populations in response to lures in different regions of the world are considered^{19,20}. Of particular interest is the development of synergistic lures that may provide high-quality attractant signals to both male and female moths, resulting in more reliable attraction under variable environmental conditions²¹. Examples of lures that act synergistically in tortricid moth species other than *G. molesta* include the work of Knight et al.¹³ and Preti et al.²², who reported the use of a 4-kairomone blend (PHEROCON MEGALURE CM 4 K DUAL, hereafter Megalure) consisting of pear ester (ethyl (*E*, *Z*)-2,4-decadienoate), acetic acid, (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) and pyranoid linalool oxide, which significantly increased catches of the codling moth *Cydia pomonella* (Linnaeus) (CM) (Lepidoptera: Tortricidae), males and females in the western USA compared with traps baited with only the CM sex pheromone.

Benzaldehyde (BEN), an aromatic compound that is released by plants largely in the Rosaceae family, has been shown to increase the response of male but not female *G. molesta* when it is added to traps baited with Megalure²³. In the same study, a 2-kairomone blend (linalool oxide and DMNT) attracted threelined leafrollers, *Pandemis limitata* (Robinson), only when BEN was added to the 2-kairomone blend. The observed differences in moth responses with and without BEN prompted us to further explore its interaction with semiochemical lures.

In this study, we examined the behavioral responses of both male and female *Grapholita molesta* to BEN, both alone and in combination with sex pheromone and the commercially available lure Megalure. The primary objective of this study was to evaluate whether BEN can increase male attraction to existing semiochemical lures and to characterize its interaction with sex pheromone across distinct seasonal periods. We sought to elucidate the types of interactions (synergistic, additive) between BEN and the *G. molesta* sex pheromone to inform the development and refinement of semiochemical-based monitoring and management strategies for *G. molesta*.

Results

2021 study

Midseason captures (17 June to 22 July). During this time period, male *G. molesta* catches were generally low, with a maximum of approximately 10 per trap, on average. Mixed-model analysis revealed a significant effect of treatment on the number of male *G. molesta* captured ($F_{7,21} = 5.1$, $P < 0.001$). Megalure traps containing BEN at a low dose (BEN-L) caught significantly more male *G. molesta* than unbaited traps did (Fig. 1A). Only BEN at a low dose (BEN-L) and Megalure alone attracted female *G. molesta* during this period (Table 1).

Across all treatments, only 14 *C. pomonella* males were captured during the midseason period (S1 Table).

Late season captures (23 July to 2 September). A significant effect of treatment was detected on male *G. molesta* captures ($F_{7,21} = 8.9$, $P < 0.001$). During this period, traps baited with a low dose of BEN (BEN-L), Megalure with BEN-L, and Megalure with a medium dose of BEN (BEN-M) captured significantly more male *G. molesta* than nonbaited traps did (Fig. 1B). All other treatments were statistically similar. Although the differences were not statistically significant, traps baited with the higher dose of BEN exhibited a numerical decrease in male *G. molesta* captures compared to the lower-dose treatments during this period (Fig. 1B). Only 10 male *C. pomonella* were captured across all treatments during this period.

Female captures were low during the late season, with a total of 10 *G. molesta* females recorded across all treatments. The highest mean capture (1.0 per trap) occurred in the Megalure + BEN-L treatment (Table 1).

2022 study

Early season captures (28 April to 8 June). *Grapholita molesta* populations peaked during this period, with 2,618 *G. molesta* (males and females) captured across all the treatments. The mixed-model analysis revealed a significant effect of treatment on the number of male *G. molesta* captured ($F_{7,28} = 24.3$, $P < 0.001$). BEN alone and in combination with Megalure was attractive to male *G. molesta*. Compared with traps baited with BEN at very low doses (BEN-VL), traps baited with Megalure and BEN-L captured significantly more male *G. molesta* (Fig. 2A). All other treatments elicited intermediate levels of male *G. molesta* attraction.

Megalure + BEN-L captured the highest number of female *G. molesta* during this period, with a numerical average of 4.6 individuals per trap (Table 1).

Only 22 male *C. pomonella* were captured across all treatments during this period (S1 Table), which was insufficient to support statistical analysis.

Midseason captures (9 June to 25 July). The number of male *G. molesta* caught in traps differed significantly among the treatments ($F_{7,28} = 32.5$, $P < 0.001$). Coinciding with the previous period, traps baited with Megalure + BEN-M captured significantly more male *G. molesta* adults than traps baited with Megalure, BEN-M, BEN-L and BEN-VL (Fig. 2B). The level of attraction of BEN to *G. molesta*, regardless of the dose, was statistically similar to that of Megalure alone. Compared with the nonbaited control, all the treatments attracted significantly more male *G. molesta*.

Female captures were minimal during this period, with only four individuals recorded across all treatments (Table 1). Similarly, a total of 45 male *C. pomonella* were captured (S1 Table), which remained insufficient for statistical analysis.

2024 study

Following the evaluation of BEN in combination with Megalure in 2021 and 2022, the 2024 study focused more specifically on characterizing the interaction between BEN and the *G. molesta* sex pheromone across different seasonal periods.

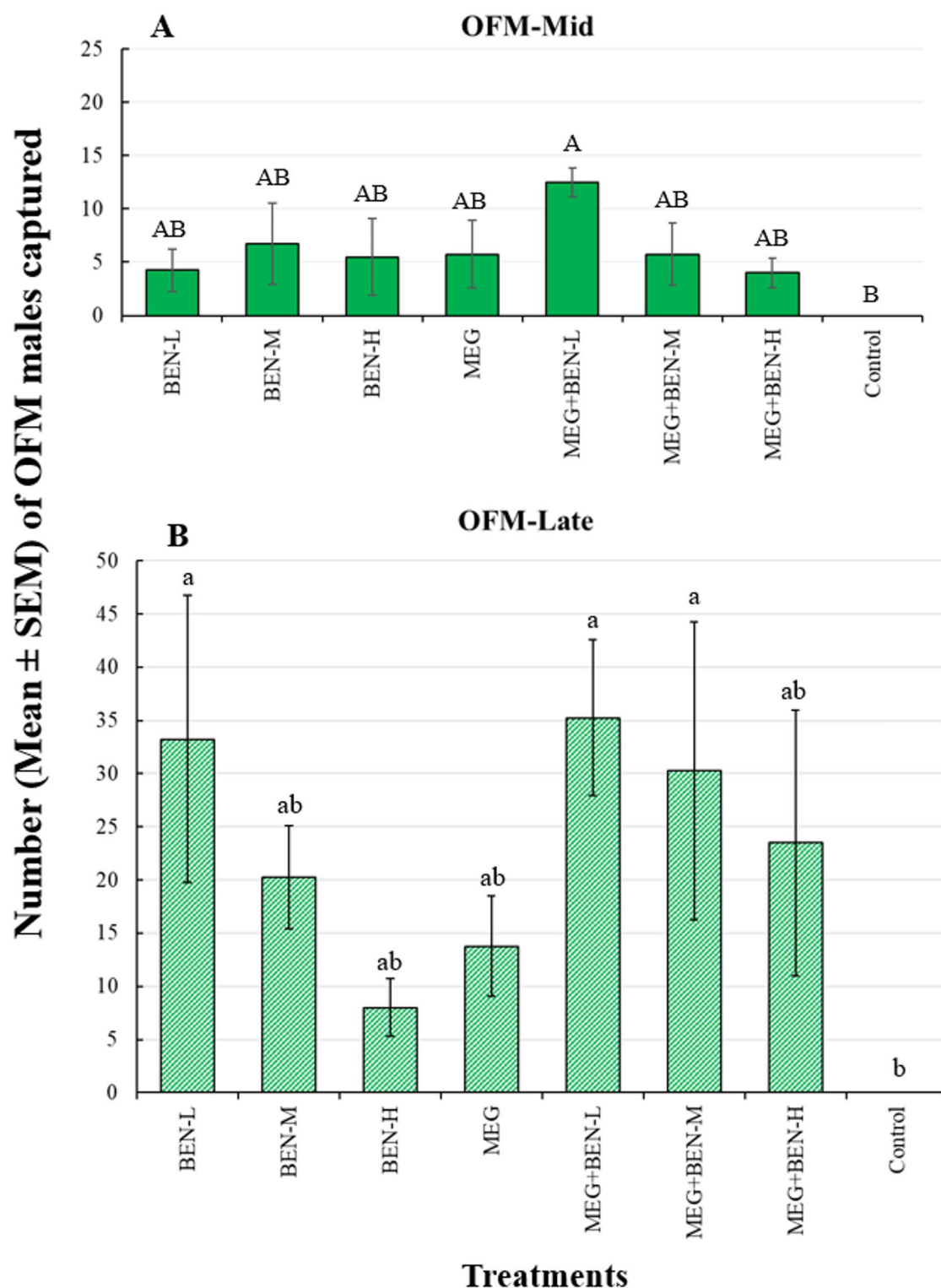


Fig. 1. 2021 captures (mean ± SEM) of male *G. molesta* in delta traps baited with seven olfactory treatments and nonbaited traps in (A) the middle season (17 June–22 July) and (B) late season (23 July –2 September). Bars superscribed with the same letter do not differ significantly among treatments (Tukey's protected HSD test, $\alpha = 0.05$).

Early season captures (30 April to 21 May). During this season, *G. molesta* populations peaked, with 67% of total male captures recorded across treatments. A mixed-model analysis indicated a significant effect of treatment ($F_{3,16} = 34.7$, $P < 0.001$), with the combination of the *G. molesta* sex pheromone and BEN capturing significantly more *G. molesta* than either BEN or pheromone alone did, whereas the captures in the BEN and pheromone

Lures	Average <i>G. molesta</i> female captures			
	2021		2022	
	Mid	Late	Early	Mid
BEN-VL	-	-	0	0
BEN-L	0.25	0	0.2	0
BEN-M	0	0	0	0
BEN-H	0	0	-	-
MEG	0.25	0.75	3.8	0.2
MEG + BEN-VL	-	-	3.4	0.6
MEG + BEN-L	0	0.25	4.6	0
MEG + BEN-M	0	0.75	3.2	0
MEG + BEN-H	0	0	-	-
Unbaited	0	0	0	0

Table 1. Mean number of female *G. molesta* captured according to the trapping period in 2021 and 2022. The release rates of benzaldehyde were 3, 6, 12, and 18 mg/day for the very low (VL), low (L), medium (M), and high (H) doses, respectively.

treatments were statistically similar (Fig. 3). ROI analysis provided evidence of an additive interaction between BEN and pheromone (Table 2).

Midseason captures (18 June to 7 July). During the middle of the season, the treatment effects remained significant ($F_{3,16} = 20.2$, $P < 0.001$), with the pheromone + BEN combination capturing more *G. molesta* than BEN, pheromone, or the control, although the captures among the BEN, pheromone, and control treatments were statistically similar (Fig. 3). ROI analysis during this period revealed a synergistic interaction between BEN and pheromone (Table 2).

Late season captures (5 August to 28 August). As shown in Fig. 3, in the late season the treatment effects were again significant ($F_{3,16} = 33.7$, $P < 0.001$), with the pheromone + BEN combination capturing the greatest number of *G. molesta*, whereas BEN and pheromone captures were statistically similar. As in the early season, the ROI analysis suggested an additive interaction between BEN and pheromone (Table 2).

Discussion

Herbivorous insects possess remarkable olfactory capabilities, allowing them to filter relevant odors from complex volatile blends emitted by host and nonhost plants^{1,24}. While a few dominant compounds typically characterize plant volatile blends²⁵, minor components often play a critical role in shaping the behavioral response^{15,26}. Our findings indicate that BEN is highly attractive to male *G. molesta* and synergistically interacts with sex pheromones during the middle of the season but has an additive effect in the early and late seasons. This finding aligns with previous research demonstrating that host-plant-derived volatiles can increase pheromone-mediated attraction in tortricid moths^{12–16}.

The combined results from 2021 to 2022 demonstrated that adding a low dose of BEN to Megalure (MEG + BEN-L) significantly increased its attractiveness to male *G. molesta*. Interestingly, in 2021, a higher BEN release rate (BEN-H) was associated with a numerical decline in *G. molesta* captures when used alone or in combination with Megalure, which contributed to its exclusion from the 2022 trials in favor of a lower-dose. This pattern aligns with findings of Piñero & Dorn¹⁵, and Piñero et al.¹⁶, who reported that lower doses of BEN elicited stronger physiological and behavioral responses in *G. molesta* females. More broadly, our work is aligned with the use of mg/day release rates as the standard for plant volatile lures, since volatiles diffuse faster than pheromone acetates. Similar BEN release rates have been reported in other insect systems, such as trapping systems for plum curculio, *Conotrachelus nenuphar*²⁷. Notably, the 2022 study showed that BEN alone, at all tested release rates, was as attractive as Megalure to males. This is the second report demonstrating a strong male *G. molesta* response to BEN, following Giri et al.²³.

Previous studies have shown that insects exhibit seasonal variations in their responsiveness to semiochemicals, potentially driven by shifts in mating behavior, host availability, or competitive pressures^{12,15,16}. In our study, trap captures consistently displayed strong seasonal patterns across all years, with markedly higher *G. molesta* catches in the early season than in the mid- and late-season periods, regardless of the lure type. This pattern is likely explained by the synchronized emergence of adults from the overwintered generation²⁸. As the season transitions, more larvae enter diapause in response to decreasing day length, creating a large spring cohort that emerges simultaneously and produces high early-season captures²⁸. Although numbers are high, these overwintered adults may also suffer fitness costs from diapause, such as reduced female fecundity, which could influence population dynamics²⁹. In subsequent generations, fewer moths emerge, naturally leading to reduced trap captures in the middle- and late-season periods. The reduced late-season captures may also be influenced by insecticide applications targeting other pests. Notably, this pattern of diminishing trap catches after the early peak is consistent with previous work in non-mating-disrupted commercial orchards, where *G. molesta* catches declined substantially beyond the overwintered-generation peak, resulting in relatively lower population levels later in the season²³. Importantly, despite these lower catches, we still detected a statistically significant

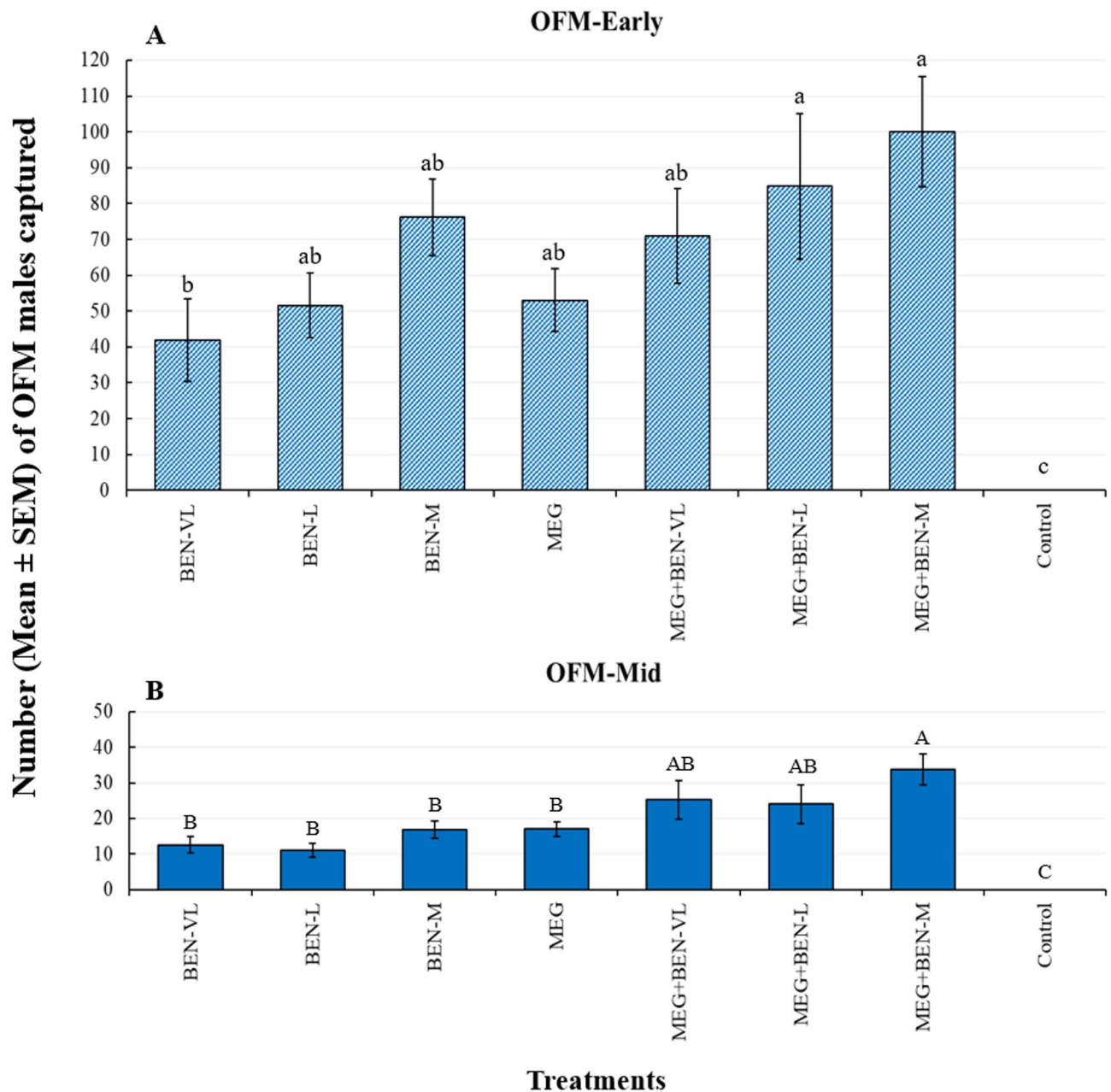


Fig. 2. 2022 captures (mean \pm SEM) of male *G. molesta* in delta traps baited with seven olfactory treatments and nonbaited traps in the (A) early-season (April 28 to June 8) and (B) midseason (July 9 to July 25). Bars superscribed with the same letter do not differ significantly among treatments (Tukey's protected HSD test, $\alpha = 0.05$).

synergistic interaction between BEN and pheromone during the mid-season, when background moth densities were reduced. While this lends confidence to the biological relevance of the interaction, we acknowledge that the robustness of conclusions drawn under low-density conditions is inherently limited. Consequently, multi-year, multi-site studies under varying pest pressures will be essential to validate and generalize the mid-season synergistic effect and to confirm how population density modulates BEN–pheromone interactions.

Benzaldehyde, a naturally occurring aromatic aldehyde, is derived from the hydrolysis of amygdalin^{30,31} and is a predominant volatile in *Prunus* spp. (Rosaceae)¹⁴. While BEN has been widely studied as a semiochemical agent in Curculionidae^{32–37}, it has also shown promising applications in Lepidoptera, including *Spodoptera litura* (Fabricius)³⁸, *Helicoverpa armigera* (Hübner)³⁹, *Pieris rapae* (Linnaeus)⁴⁰, and *Manduca sexta* (Linnaeus)⁴¹. The increased attraction observed when BEN is combined with sex pheromones suggests that this compound may play a role in mimicking host cues that amplify pheromone responses. From a practical perspective, our results suggest that BEN could be a valuable addition to existing lures, particularly when it is used at optimal dosages and for seasonal timings.

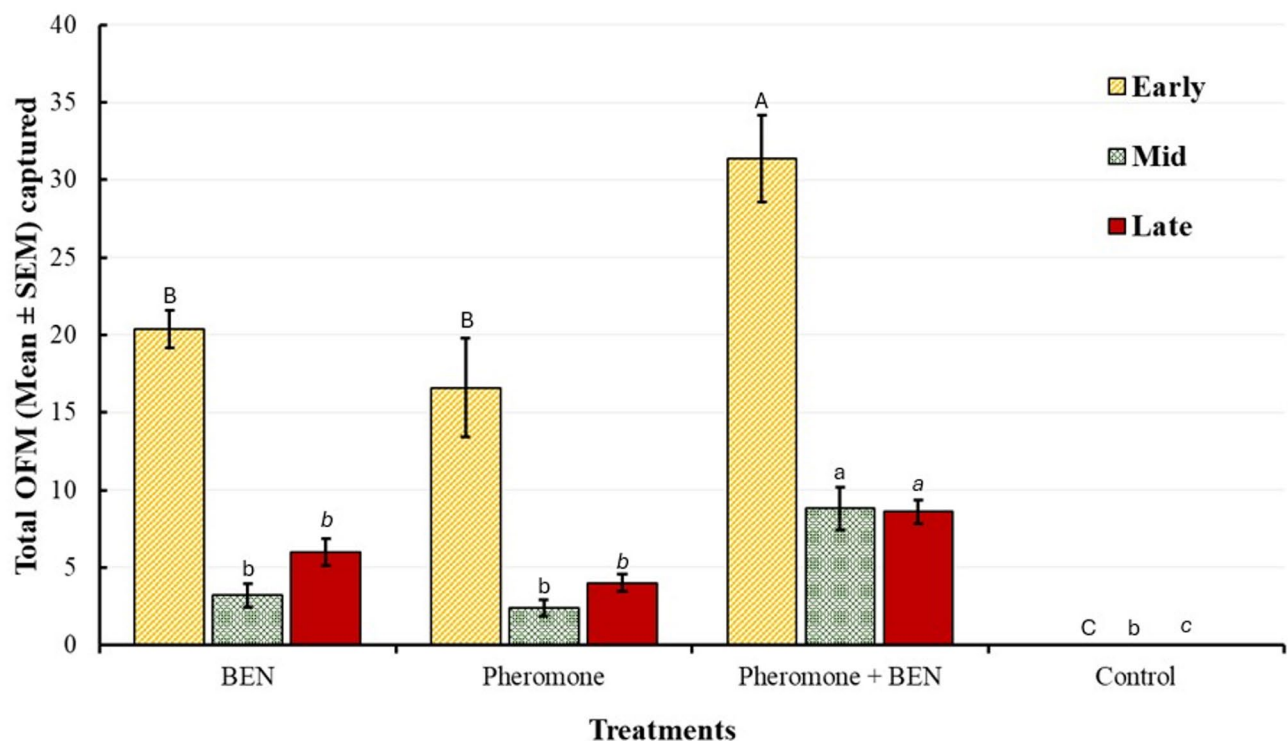


Fig. 3. 2024 captures (mean \pm SEM) of male *G. molesta* in delta traps baited with three olfactory treatments and nonbaited traps in the early season (30 April – 21 May, dotted yellow bars), mid-season (18 June–9 July, green dotted bar), and late season (5 August–28 August, solid red bar). Statistical analyses were conducted within each season separately. Different letters above bars indicate significant differences among treatments within the same season (Tukey's HSD test, $\alpha = 0.05$): uppercase letters for early season, lowercase for mid-season, and italicized lowercase for late season.

Season (2024)	Chemical	Ratio of interaction (ROI) ^a	Type of interaction
Early	Pheromone + BEN	0.87 \pm 0.13	additive
Mid	Pheromone + BEN	1.55 \pm 0.12 *	Synergistic
Late	Pheromone + BEN	0.85 \pm 0.03	additive

Table 2. Types of interactions observed between single attractants (Pheromone or BEN) and combined attractants (Pheromone + BEN) across early, middle, and late seasons (2024), as determined by ratios of interaction. Pheromone = OFM L2 (*G. molesta* sex pheromone); BEN = Benzaldehyde. ^a Mean \pm SE. * $P < 0.05$ for the null hypothesis that the ratio of interaction (ROI) = 1 (Hammack, 1996)⁵¹, according to a two-tailed *t* test (*df* = 4).

Benzaldehyde alone was shown to be as attractive to male *G. molesta* as a sex pheromone across the entire growing season in 2024. However, its interaction with the pheromone varied seasonally, exhibiting additive effects in the early and late seasons but a synergistic effect in the middle of the season. The additive effect observed early in the season, despite high *G. molesta* populations, might be due to a 'dilution' effect of naturally emitted BEN from apple flowers, which peaks during petal fall^{42,43}. As the season progresses, BEN emissions from fruit-bearing twigs steadily decline⁴³. This may explain the synergistic interaction observed in the middle of the season when background levels in the orchard atmosphere are relatively low. In contrast, the late-season additive effect may be attributed to shifts in the volatile profile of the orchard as the fruit ripens. During this period, emissions of esters and alcohols increase, while aldehyde levels, including BEN, decrease⁴³. This shift may result in reduced interference with the synthetic BEN in traps, maintaining an additive rather than a synergistic response.

The incorporation of BEN into monitoring or control systems may enhance male responsiveness, particularly during the middle of the season, when synergistic effects are noted. While *G. molesta* sex pheromone lures that are specifically designed for use in mating disruption orchards already exist^{44,45}, BEN may be a promising candidate for additional trials aimed at improving detection sensitivity in these settings. Its demonstrated attractiveness, alone and in combination with the pheromone, suggests potential utility for improving trap performance under conditions where pheromone-based communication is disrupted. Furthermore, its integration into attract-and-

Lures	Active compounds	Matrix	Release rate	Longevity
1 Megalure CM 4 K Dual *	ethyl (E, Z)-2,4-decadienoate (pear ester); acetic acid; (E)-4,8-dimethyl-1,3,7-nonatriene (DMNT); and 2,2,6-Trimethyl-6-vinyltetrahydro-2 H-pyran-3-ol (pyranoid linalool oxide, PyrLOX)	Acetic acid loaded in membrane cup. All other lures in Poly vinyl chloride (PVC).	Not specified	8 weeks
2 Pherocon * OFM L2	(Z)-8-Dodecenyl acetate; (E)-8-Dodecenyl acetate; and (Z)-8-Dodecenol loaded in a grey halobutyl rubber septa.	Rubber Septa	0.96 µg/day	8 weeks
3 Benzaldehyde Very Low	Benzaldehyde	PVC	3 mg/day	8 weeks
4 Benzaldehyde Low	Benzaldehyde	PVC	6 mg/day	8 weeks
5 Benzaldehyde Medium	Benzaldehyde	PVC	12 mg/day	8 weeks
6 Benzaldehyde High	Benzaldehyde	PVC	18 mg/day	

Table 3. Description of the semiochemical lures used in field trials, including lure composition, formulation matrix, release rates (where applicable), and field longevity. Release rates and longevity values are based on manufacturer specifications. Only benzaldehyde lures were independently confirmed for their release rate in this study.

kill strategies could contribute to population suppression by diverting males away from mating opportunities (El-Sayed et al., 2006)¹⁰.

Female *G. molesta* were captured in low numbers across all study years, with a greater response to Megalure than to BEN alone. This aligns with findings by Piñero & Dorn¹⁵, Piñero et al.¹⁶, and Xiang et al.⁴⁶, which suggest that BEN primarily acts as a male attractant. Similarly, Luo et al.⁴⁷ demonstrated that while BEN could be detected in female *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), it was insufficient to elicit a behavioral response unless it was presented in a multicomponent blend.

Conclusions

Our findings demonstrate that (1) BEN is a potent male attractant to a level that is comparable to the Megalure or OFM sex pheromone, (2) adding BEN at low or medium doses to these lures enhances male captures without affecting females, and (3) BEN interacts with the OFM pheromone in a season-dependent manner, showing synergism in the middle-season and additive effects in the early and late seasons. These results highlight benzaldehyde’s role in enhancing pheromone-based attraction without additional host volatiles, offering a valuable tool for improving pest monitoring and management. The incorporation of BEN into existing lures could optimize attractants on the basis of seasonal population dynamics.

Future research should elucidate the neural and behavioral mechanisms underlying these effects and assess BEN–pheromone blends with other semiochemicals, under varying field conditions. From an applied perspective, optimizing release rates and dispenser types could further refine their application in integrated pest management.

Materials and methods

Study site

Field-scale studies were conducted over a 3-year period (2021, 2022 and 2024) at the University of Massachusetts Cold Spring Orchard Research and Education Center in Belchertown, MA. The 2021 study was carried out from 17 June to 2 September, the 2022 study was carried out from 28 April to 25 July, and the 2024 study was carried out from 30 April to 28 August. This orchard received a standard insecticide spray program against key pests such as plum curculio (PC), *Conotrachelus nenuphar* (Herbst) (Coleoptera: Curculionidae), and apple maggot fly (AMF), *Rhagoletis pomonella* (Walsh) (Diptera: Tephritidae). No insecticides were sprayed against any other insect pests. Fungicides to control scab and other summer diseases were applied as necessary by the growers. The cultivars most commonly present in the test blocks were McIntosh, Empire, Red Delicious, Gala, Ginger Gold, and Cortland on the M.26 and M.7 rootstocks.

Odor treatments and trap deployment

For the 2021 study, the following olfactory treatments were evaluated: (1) Benzaldehyde (BEN) low dose (BEN-L), (2) BEN medium dose (BEN-M), (3) BEN high dose (BEN-H), (4) Megalure CM 4 K Dual (hereafter referred to as Megalure), (5) Megalure + BEN-L, (6) Megalure + BEN-M, and (7) Megalure + BEN-H. The treatments evaluated in 2022 were (1) BEN very low dose (BEN-VL), (2) BEN-L, (3) BEN-M, (4) Megalure, (5) Megalure + BEN-VL, (6) Megalure + BEN-L, and (7) Megalure + BEN-M. The treatments evaluated in 2024 were (1) BEN-M, (2) Pherocon OFM L2 (pheromone), and (3) pheromone + BEN. The release rates of the various dosages of BEN were determined gravimetrically (at 25 °C) to be 3, 6, 12, and 18 mg/day for very low, low, medium, and high release rates, respectively. For all the study years, unbaited traps served as negative controls. Each treatment was replicated 4 times in 2021 and 5 times in 2022 and 2024. Refer to Table 3 for detailed information on lure chemical composition, field longevity, and release rates.

All lures were placed inside orange-colored delta-shaped traps (Pherocon VI, Trécé Inc., Adair, OK, USA) containing liners coated with cold-melt adhesive⁴⁸. The experimental lures were formulated by Trécé, Inc., in a proprietary black polyvinyl chloride (PVC) matrix. The traps were spaced at 15-m intervals along the perimeter of the apple blocks and were suspended from the upper third of the tree canopy. During trap set-up, the relative position of each treatment was randomized within each experimental block. The traps were rotated weekly

clockwise within a replication to minimize the effect of position. All lures were renewed at 6-week intervals, and the sticky liners were replaced every 4 weeks.

Data collection

For the 2021 study, traps were examined beginning on 24 June and then weekly until 2 September. For the 2022 study, traps were examined beginning on 5 May and then weekly until 25 July. For the 2024 study, traps were examined beginning on 30 April and then weekly until 28 August. All the captured adult moths were identified to species and placed in 25 ml glass vials containing 70% ethanol. The sex of each moth species was identified according to Fuková et al.⁴⁹ and Shang et al.⁵⁰ by examining the genitalia under a dissecting microscope (S1 Fig).

Statistical analysis

The number of male and female moths captured per trap per week was used as the dependent variable for the analyses. A preliminary analysis using repeated-measures ANOVA of trap-capture data from *G. molesta* (males only) revealed a significant interaction in all three years. This interaction indicated differential responses by the male moths to the treatments over time. Therefore, moth captures were divided into two seasonal time periods in 2021 (midseason: 17 June–22 July, and late season: 23 July–2 September), two seasonal time periods in 2022 (early season: 28 April–8 June, and midseason: 9 June–25 July) and three seasonal time periods in 2024 (early season: 30 April–21 May, midseason: 18 June–9 July, and late season: 5 August–28 August). For each year, the number of male *G. molesta* captured in each period was analyzed via generalized linear mixed models with a Poisson distribution, which assessed the effects of ‘treatment’ (fixed effect) and ‘replicate’ (random factor) and the 2-way interactions among them. Overdispersion was tested by examining the deviance goodness-of-fit test via a log link function. For all analyses, the data were transformed to $(x + 0.5)^{1/2}$ prior to analysis to stabilize variances. Where appropriate, treatment means were compared using Tukey’s protected HSD test ($\alpha = 0.05$).

In 2024, in addition to ANOVA, we performed comparisons of ratios of interaction (ROIs)⁵¹ to examine the type of interaction (inhibitory, additive, or synergistic) among single- versus 2-component odor treatments. In our case, an ROI = [(pheromone + BEN) + Control] / [(Pheromone) + (BEN)], where (pheromone) represents *G. molesta* captures by traps baited with OFM L2 sex pheromone lure, (BEN) represents the capture of *G. molesta* by traps baited with BEN, (pheromone + BEN) denotes *G. molesta* captured by traps baited with OFM sex pheromone and BEN together, and the control represents the nonbaited traps. ROI values significantly less than, equal to, or greater than 1 corresponded to inhibitory, additive, or synergistic interactions, respectively, between odor components^{27,51}. Each ROI value was derived from one of the five replicates performed for each odor group. A two-tailed Student’s t test using such ROI values was subsequently performed to test the null hypothesis of ROI = 1 for each odor evaluated.

All the statistical analyses were performed via STATISTICA v.13 (TIBCO Software Inc., Palo Alto, CA, USA)⁵². Female *G. molesta* and *C. pomonella* captures were not analyzed statistically because of insufficient numbers.

Data availability

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

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Author contributions

J.C.P., A.G. and B.S. conceived the experiments; A.G. conducted the experiments; J.C.P. and A.G. analyzed the results. B.S. equally contributed to the syntheses of results and discussion. All authors reviewed the manuscript.

Declarations

Competing interests

The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to J.C.P.

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