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A meta-analytic investigation of the potential for plant volatiles and sex pheromones to enhance detection and management of Lepidopteran pests

Review Article

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Abstract

Effective early detection, monitoring and management methods are critical for reducing the impacts of insect pests in agriculture and forestry. Combining host plant volatiles with sex pheromones could enhance trapping methodologies, whilst the use of non-host volatiles could improve the effectiveness of pest management through repellency effects. In this meta-analysis approach, we analysed 51 studies that used electroantennograms (EAG), wind tunnels and/or field traps to evaluate the antennal and behavioural responses of Lepidoptera to sex pheromones combined with attractant or repellent plant volatiles. Proposed attractant plant volatiles had a positive association with female Lepidoptera responses to sex pheromone, but effects on males were highly variable, with unexpected repellency reported in some studies. Proposed repellent plant volatiles were significantly or near-significantly negatively associated with male attraction to sex pheromones but were scarcely studied. Sub-group analysis identified that male responses to sex pheromone were reduced when the dose of attractant plant volatile relative to sex pheromone was increased. Green-leaf volatiles were associated with the strongest positive effects for males in field traps. Multiple-compound attractant plant volatile blends were less effective than single compounds in field studies. Our analysis demonstrates, (i) the potential value of combining host plant volatiles with sex pheromones to capture females rather than only males, (ii) the importance of identifying appropriate host plant volatiles and optimal relative doses, and (iii) the potential for non-host plant volatile use in pest management strategies.

Introduction

Insect pests have major economic and environmental impacts within both forestry and agricultural systems worldwide (Culliney, 2014; van Lierop *et al.*, 2015), which is predicted to be exacerbated because of projected climate change scenarios and increased risk of the establishment of non-native invasive species through global trade (Deutsch *et al.*, 2018; Lehmann *et al.*, 2020). The identification of pheromones and plant volatile chemicals which may attract or repel insect pests is a critical research area that could facilitate the development of more effective early detection and monitoring tools and improved or alternative management approaches (Larson *et al.*, 2020; Mafra-Neto *et al.*, 2022). In the Coleoptera, for example, successful applications of plant volatiles in insect pest management include the combination of a host plant volatile with a sex pheromone to attract emerald ash borer *Agrilus planipennis* Fairmaire to traps (Ryall *et al.*, 2012; Wittman *et al.*, 2021), and anti-aggregation pheromones combined with non-host volatiles to repel mountain pine beetle *Dendroctonus ponderosae* Hopkins from forestry crops (Fettig and Munson, 2020).

Lepidoptera (butterflies and moths) include many of the most serious pests of plants and have been reported to make up eight of the top 20 most studied arthropod pests, which includes diamondback moth *Plutella xylostella* L., cotton bollworm *Helicoverpa armigera* Hübner and codling moth *Cydia pomonella* L. (Willis, 2017). Plant volatile lures, typically derived from the insect's favoured host plant species, have previously been shown to be effective in attracting adult Lepidoptera, especially females (Szendrei and Rodriguez-Saona, 2010). Furthermore, the identification of sex pheromones for many Lepidopteran pest species in recent years has led to the development of effective species-specific traps, although these typically only catch males (Witzgall *et al.*, 2010; Rizvi *et al.*, 2021). The combination of host plant volatile lures with sex pheromones therefore has potential to improve capture rates of males whilst also attracting females, on the premise that females are attracted to volatiles associated with favoured host plants, and males are attracted to females located on optimal hosts (Reddy and Guerrero, 2004; Szendrei and Rodriguez-Saona, 2010; Bruce and Pickett, 2011; Xu and Turlings, 2018). In addition, the identification of non-host plant volatiles which repel pests could lead to more effective management options, such as 'push–pull' strategies which aim to 'push' pests away from high priority areas using repellent plant volatiles or appropriate non-host plants, whilst simultaneously using attractant volatiles to 'pull' the target pest into traps or to lower-risk areas (Cook *et al.*, 2007; Eigenbrode *et al.*, 2016).

Early studies in the 1980s and 1990s found that combining host plant volatiles with sex pheromone lures did improve capture rates of male moths compared with pheromone-only lures (reviewed in Landolt and Phillips, 1997). A number of subsequent studies, however, have found that proposed attractant plant volatiles unexpectedly reduce male capture rates (e.g. Meagher, 2001; Hu *et al.*, 2013; Barros-Parada *et al.*, 2018) or fail to catch females (Tang *et al.*, 2012). Several possible explanations have been suggested to explain the variable effectiveness of candidate attractant plant volatiles. The choice of host plant volatile used within combined lures is an important factor which depends on target species (e.g. Tang *et al.*, 2012; Hu *et al.*, 2013; Mujica *et al.*, 2018), and in some cases effects have been classified according to the type of compound such as green leaf volatiles, floral aromatics or terpenes (Fang *et al.*, 2018). In addition, the dosage of host plant volatiles and their ratio to the sex pheromone has been shown to be an important factor in some cases, with several studies demonstrating that the dosage of plant volatile can determine whether there is an attractant or repellency effect of a certain plant volatile on male response of a target species to its sex pheromone (e.g. Hu *et al.*, 2013; Yu *et al.*, 2015; Xiang *et al.*, 2019). In the field, trap design can also influence the effectiveness of combined lures (Gregg *et al.*, 2018), because trapping area (i.e. the trap's behaviourally effective plume reach) could depend on trap type, and a plant volatile which is attractive at distance could act as a repellent at close proximity to the insect (Kvedaras *et al.*, 2007). Other factors which might conceivably influence the effects of plant volatiles combined with sex pheromones include (i) host specialism of the target species, since host-specialists might be more attracted to or repelled by particular volatiles; (ii) blend complexity, given that blends of host volatiles are often more attractive than a single component (Gregg *et al.*, 2018); and (iii) habitat, given that background odour influences the interaction between plant volatiles and pheromones (Cai *et al.*, 2017). However, these factors have yet to be systematically investigated in the context of combining plant volatiles with sex pheromone lures.

The current lack of systematic evidence to explain why host plant volatiles can unexpectedly reduce the attraction of male Lepidoptera to sex pheromones and/or fail to attract females, and whether non-host volatiles can repel male Lepidoptera from sex pheromones, is a constraint to ongoing research of pest management strategies for some Lepidoptera species. As such, the aim of this study was to evaluate the effect of proposed attractant or repellent plant volatiles on the antennal and behavioural responses of adult Lepidoptera to sex pheromone in laboratory and field studies. In addition, we considered which factors might be most important in designing effective combined pheromone-plant volatile lures, by evaluating the influence of plant volatile category, plant volatile blend complexity, ratio of the plant volatile to sex pheromone, host specialism of the target insect, habitat type and trap type, on the attraction of male Lepidoptera to plant volatiles. We also investigated spatial patterns of attraction of males and females to combined pheromone–plant volatile lures in wind tunnels. We then discuss how our findings relate to previous studies which have investigated the effects of plant volatiles alone (e.g. Szendrei and Rodriguez-Saona, 2010).

Materials and methods

Literature search

A search of the literature was undertaken using Scopus in early 2022. The following search term was used within article title, abstract and keywords: pheromone AND (volatile OR kairomone OR allomone OR semiochemical) AND ('wind tunnel' OR olfactometer OR EAG OR electroantennogram OR trap*). Studies were initially screened by reviewing their titles, abstracts and main text as appropriate, and included in the meta-analysis if they met all of the following criteria: (i) results presented for a species of Lepidoptera; (ii) the study compared the effects of plant volatile (s) combined with a conspecific sex pheromone simultaneously at the same source, vs. a sex pheromone-only control, on the response of the target species. The two treatments otherwise comprised exactly the same specifications (e.g. trap type) and the same sex pheromone constituents; (iii) for field trapping, sites which were not under mating disruption or sterile moth release treatments; (iv) sufficient text in English to decipher the results, and (v) adequate and clearly presented statistical information (e.g. means, standard errors and sample sizes) for inclusion in the meta-analysis models. Studies which failed the final criterion were included in the Discussion. A non-systematic supplemental search of Google Scholar was also undertaken to identify any additional references including grey literature. Upon completion of the systematic search, references cited in the most recent publications were screened to obtain any additional relevant studies.

Volatiles which were tested as both attractants (e.g. host volatiles) and repellents (e.g. non-host volatiles) were included but were analysed separately. Both male and female adult Lepidoptera were included. The literature search was global with no geographic restrictions. We aimed to include behavioural laboratory studies such as electroantennogram (EAG) responses, choice experiments such as olfactometers and wind tunnels, in addition to field-trapping studies. However, only three choice experiment publications were identified (Xiao *et al.*, 2002; Ma *et al.*, 2016; McCormick *et al.*, 2017), therefore, this method was not included in the meta-analysis.

A total of 1699 publications were returned by the search term. The majority of these did not report data for Lepidoptera. Therefore, after screening according to the above criteria, 51 studies were selected for inclusion in the meta-analysis (listed in Supplementary Material 1), comprising nine EAG studies, 23 wind tunnel studies and 35 field-trapping studies (note that some of the 51 studies included more than one method).

Calculation of effect sizes

Data were extracted from each publication and compiled into separate databases for EAG, wind tunnel and field-trapping studies. Where necessary, data were extracted from figures using WebPlotDigitizer Version 4.5 (Rohatgi, 2021). The response of Lepidoptera to combined plant volatile–sex pheromone lures vs. pheromone-only lures was measured as follows according to each experimental method: for EAG studies, response was measured as electrical antennal signal (which could equally represent an attractant or repellent response); for wind tunnel studies, response was measured as the number of individuals achieving a certain stage in the tunnel (e.g. take-off, half-way, approach to lure; recorded in separate rows); and for field-trapping studies, the response was defined as the number of individuals captured in traps. Sex of the target insect was recorded, where stated.

Where no female captures were reported, the entire paper was reviewed for any reference to female captures; if the paper stated that no females were captured, this was added into the effect size database for each experiment.

All analysis was undertaken using the ‘metafor’ package (Viechtbauer, 2010) in R version 4.0.2 (R Core Team, 2020). Effect sizes were calculated using standardised mean difference (Hedges, 1981) for EAG and field studies, or log odds ratio for wind tunnel studies because of the proportion data. The ‘treatment’ was insect response to the combined plant volatile and pheromone lure, and the ‘control’ was response to the pheromone-only lure.

Meta-analysis models

Meta-analysis models were built using the ‘rma.mv’ function in the ‘metafor’ package. To account for the non-independence of experiments and studies, a hierarchical random-effects structure was specified comprising each effect size nested within experiment number (where specified), nested within study ID. In addition, for wind tunnel data, stage of the wind tunnel (e.g. take-off, halfway, approach to lure) was nested within experiment number. Confidence intervals and significance tests were calculated using the t-distribution, which is more conservative than the Z-distribution with less risk of Type I error.

Initially, overall meta-analysis models were built to test the effect of attractant or repellent plant volatiles on adult Lepidoptera responses to sex pheromone according to each of the three methods (EAG, wind tunnel and field trapping). Subgroup analysis was then used to investigate causes of inconsistent effects among studies (i.e. heterogeneity) for attractant volatiles.

Subgroup analysis

Subgroup analysis was performed to identify any differences in responses to combined vs. pheromone-only lures according to sex, host specialism, trap type, habitat, complexity of the volatile blend, ratio of plant volatile to pheromone and type of volatile chemical. These subgroups were selected based on their expected influence on effect sizes, either hypothetically or from previous evidence (as explained in the Introduction). A separate model was built for each subgroup and method (EAG, wind tunnel, field trapping), because different data subsets were needed for each subgroup (table 1). In each model, the subgroup was specified as a moderator in the model.

In each subgroup model, the intercept term was removed to provide effect sizes for each level. Data were filtered to only include males (apart from the sex subgroup), because males and females responded differently, and males were much better represented in the data than females. The significance of levels within each subgroup was tested using the omnibus moderator test in the metafor package for models with the intercept term included, to test the null hypothesis that the subgroup has no influence on effect sizes.

In addition, sex-specific differences in responses to combined attractant lures vs. pheromone-only lures at varying stages in wind tunnels were analysed by including the interaction between

Table 1. Subgroup analysis for attractant plant volatiles, showing the subsets of data applied to each subgroup and level of replication

			Number of data points (and studies)		
Subgroup	Levels	Data subset	EAG	Wind tunnel	Field trapping
Sex	Male	Excludes unsexed data	87 (9)	807 (21)	213 (27)
	Female		39 (2)	129 (3)	134 (20)
Plant volatile blend	Single	Males	78 (8)	572 (17)	143 (23)
	Multiple		9 (4)	235 (13)	70 (15)
Habitat	Agriculture (herbaceous crops)	Males	N/A	N/A	108 (12)
	Forest				19 (4)
	Orchard				86 (13)
Specialism	Generalist	Males	30 (4)	352 (10)	86 (14)
	Specialist		57 (5)	455 (11)	127 (13)
Trap type	Delta	Males	N/A	N/A	73 (14)
	Inverted cone				10 (2)
	Panel				2 (1)
	Unitrap				22 (3)
	Water trap				100 (6)
Plant volatile category	Fruit volatile	Males, excludes blends of >1 type	0	13 (2)	18 (5)
	Green leaf volatile (GLV)		34 (5)	256 (14)	83 (12)
	Homoterpene		0	14 (3)	1 (1)
	Monoterpene/oid		16 (5)	100 (11)	18 (6)
	Organosulphur		0	0	3 (1)
	Phenylpropanoid		22 (4)	125 (9)	28 (7)
	Sesquiterpene		7 (2)	68 (7)	7 (2)
Ratio (standardised amount of plant volatile (PV) per unit of sex pheromone (SP))	PV:SP > mean[a]	Males, experiments where >1 ratio tested	18 (2)	123 (10)	50 (13)
	PV:SP < mean[a]		56 (2)	370 (10)	73 (13)

[a] Mean ratio calculated separately for each study.

sex and wind tunnel stage as a moderator, with the intercept removed.

Subgroup data were extracted from each publication where provided. Specialism was classified according to the main host range of the study species according to CABI's Invasive Species Compendium (CABI, 2022), with other sources used where necessary (Supplementary Material 2). Specialists were defined as having main host plants within one taxonomic family, while generalists had main hosts within more than one taxonomic family. Plant volatile types were classified into seven categories (table 1) based on their chemical composition. Values for ratio of plant volatile to sex pheromone were quantified by standardising the amount of plant volatile per one equivalent unit of sex pheromone. This quantity varied enormously among studies, therefore, the amount of plant volatile relative to sex pheromone was further standardised within each study using the 'scale' function in R.

Sex ratios

Ratios of female to male Lepidoptera were calculated for each field-trapping study which reported data for both sexes. The effect of combined attractant lures vs. pheromone-only lures on sex ratio was tested using a mixed model in the 'lme4' package (Bates *et al.*, 2015), where the sex ratio was $\log(x+1)$ transformed to account for positive skew. Random effects comprised experiment number nested within study ID. Marginal means were calculated using the 'emmeans' package (Lenth, 2021) and back-transformed.

Publication bias

Publication bias was assessed by visual inspection of funnel plots, and via a multilevel meta-regression model with the square-root of the inverse effective sample size as a moderator. This model tests whether larger effect sizes are associated with larger standard errors, which would indicate publication bias (Nakagawa *et al.*, 2022). Evidence of publication bias was found for the EAG models according to both funnel plots and the standard error moderator models, although given that only nine studies were available for this method, the apparent publication bias could be a chance effect. Therefore, the findings for the EAG models are presented as preliminary results, which require further research.

Influential cases

The influence of individual effect sizes on the model outputs was tested by calculating DFBETAS values in the 'metafor' package. In accordance with the guidance for this function, DFBETAS values greater than 1 were considered to be influential effect sizes. This was detected in one model, the sex subgroup model for EAG studies. Omitting the five influential effect sizes from this model did not substantially alter the results; the moderator and each sex were still significant and the contrast between the sexes was greater. Therefore, the full model is presented.

Results

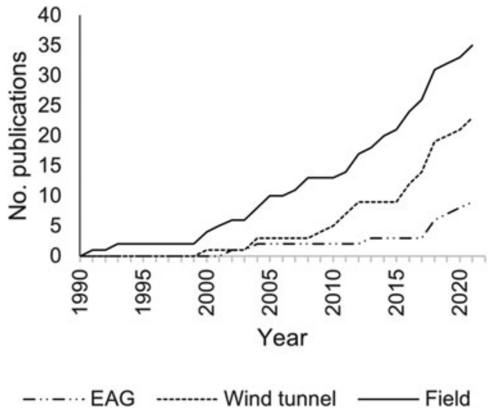

Figure 1. Cumulative number of studies included in the meta-analysis by publication date, for the three different methods (electroantennogram, wind tunnel and field trapping). Each study reported the effects of combined sex pheromone and plant volatile lures vs. pheromone-only lures on antennal or behavioural responses of Lepidopteran pests.

A total of 1561 effect sizes were extracted from 51 studies, comprising 126 from nine EAG studies, 993 from 23 wind-tunnel studies and 442 from 35 field-trapping studies (note that some papers fell into more than one category). The majority of these studies reported effects for plant volatiles tested as attractants, while only three wind tunnel studies and four field-trapping studies tested proposed repellents. The number of publications rose sharply after 2010 (fig. 1). The publications reported data from a total of 27 Lepidopteran species, comprising six in EAG studies, 15 in wind tunnel studies and 21 in field-trapping studies. The most frequently studied species were oriental fruit moth *Grapholita molesta* Busck (included in 11 of 57 studies) and codling moth *C. pomonella* L. (10 of 57 studies). The field-trapping data originated from 11 countries across Asia (14 studies), North America (14 studies), Europe (4 studies), Australia/New Zealand (2 studies) and South America (1 study).

Attractant plant volatiles had a significant positive association with Lepidoptera responses (both sexes) to sex pheromones in field-trapping studies (effect size 0.210 ± 0.069 SE, $t = 3.028$, P-value = 0.003) and in the more limited number of EAG studies (effect size 1.347 ± 0.395 SE, $t = 3.413$, P-value < 0.001), but the effect was not significant in wind tunnel studies (0.241 ± 0.149 SE, $t = 1.619$, P-value = 0.106). Repellents had a significant negative association with male Lepidoptera responses to sex pheromone lures in wind tunnels (effect size −1.120 ± 0.177 SE, $t = -6.338$, P-value < 0.001), and a near-significant negative association with male capture rates in pheromone traps in the field (−1.243 ± 0.646 SE, $t = -1.924$, P-value = 0.062). No data on combining repellents with sex pheromones were available for EAG studies or for females.

There was significant heterogeneity in the effect of combined attractant lures (i.e. plant volatile and pheromone) vs. pheromone-only lures on adult Lepidoptera responses, for all three methods (EAG: $Q = 609$ (df = 125), P-value < 0.001; wind tunnel: $Q = 3702$ (df = 935), P-value < 0.001; field trapping: $Q = 669$ (df = 352), P-value < 0.001), indicating that variation in effect sizes was greater than expected based on sampling error alone. Subgroup analysis explained some of this variability, demonstrated by the significant moderator tests for five of the seven subgroups, according to at least one method (fig. 2). The five significant effects comprised; (1) females responded more strongly than males to the combined lures compared with sex pheromone lures alone, which was consistent across all three methods (EAG, wind tunnel and field trapping) but only significant for field trapping; (2) significant differences among plant

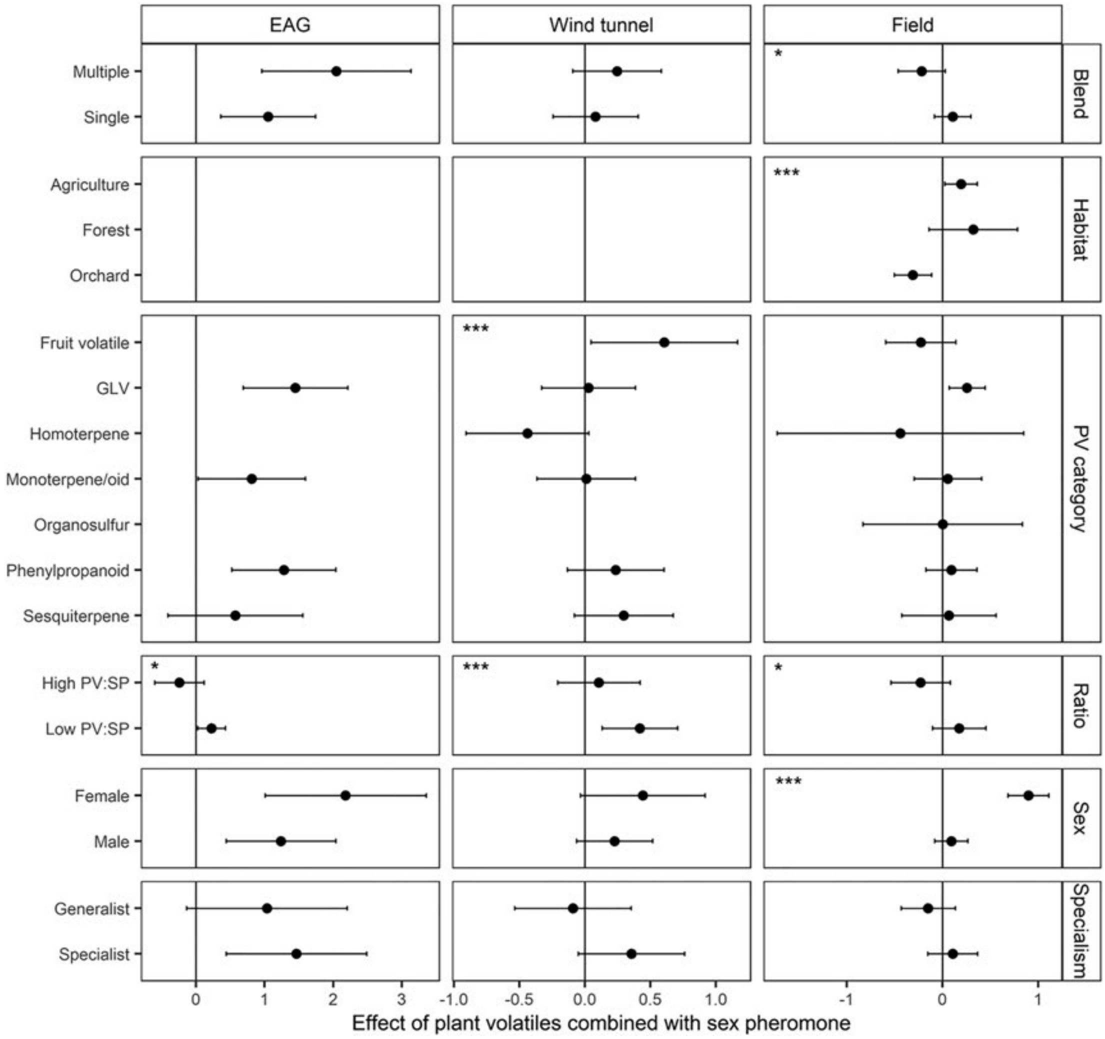

Figure 2. Effect (with 95% confidence intervals) of combined attractant plant volatile and sex pheromone lures, vs. pheromone only lures, on the responses of adult Lepidoptera according to six subgroups (rows) and three methods (columns). Positive effects represent higher responses to the combined lures compared with pheromone-only lures. One subgroup, trap type in field-trapping studies, is not shown because none of the levels were significant and the results were not informative. Data were filtered according to each subgroup, as shown in table 1. Asterisks denote where there was a significant difference between levels of the subgroup (*F* test, with intercepts), where ***$P < 0.001$, **$P < 0.01$ and *$P < 0.05$. PV, plant volatile; SP, sex pheromone.

volatile categories on male responses to sex pheromone in wind tunnels, where fruit volatiles were associated with the strongest attraction effects. In field traps, effect sizes were significantly higher for green leaf volatiles, although plant volatile category was not significant overall; (3) significantly stronger effects of male responses to combined host plant volatiles with pheromone lures vs. pheromone-only lures in agricultural rather than orchard habitats; (4) significant effects of blend complexity on male responses to combined lures in the field, with stronger attractant effects associated with single-component plant volatile blends; and (5) significantly stronger associations of male responses to sex pheromone when combined with lower doses of plant volatiles across all three methods (EAG, wind tunnel and field trapping). Trap type and host specialism were not significant sub-groups for any method, although consistently stronger associations of male responses to combined lures were observed in specialist rather than generalist species across methods.

Captures in field traps were dominated by males in both the pheromone-only and combined lures, although the latter captured significantly higher proportions of females ($t = 3.767$ ($\mathrm{df} = 205.7$), *P*-value < 0.001). Estimated marginal mean sex ratios were 0.051 females per male in pheromone-only traps, increasing to 0.100 females per male in the combined lure traps.

A comparison of sex-specific responses within wind tunnels revealed a strong differentiation in female responses to combined plant volatile and sex pheromone vs. pheromone-only sources at the activation and take-off stages (fig. 3). By contrast, significant differences in male responses to combined vs. pheromone-only lures were only seen at the final approach stage (fig. 3).

Discussion

The indications from our meta-analysis study highlighted that proposed attractant plant volatiles had a significant positive association with adult Lepidoptera responses to sex pheromones in EAG and field-trapping studies. Similarly, proposed repellents, such as non-host volatiles, had a significant negative association with male responses to sex pheromones in wind-tunnel trials, and a near-significant negative association in field-trapping studies, although only three and four studies were available, respectively.

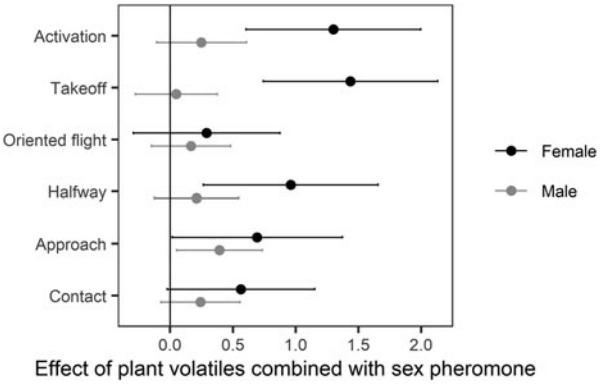

Figure 3. Effect (with 95% confidence intervals) of combined attractant plant volatile and sex pheromone lures, vs. pheromone-only lures, on male and female Lepidoptera according to wind tunnel stage. Positive values are associated with stronger effects of the combined lure vs. the pheromone.

A number of sub-group factors significantly influenced the effect of combined attractant plant volatile–sex pheromone vs. pheromone-only lures across EAG, wind tunnel and field-trapping studies (fig. 2): (i) responses of females to the combined vs. pheromone-only lures were consistently stronger than males (but only significantly so in field-trapping studies), (ii) lower ratios of plant volatile to sex pheromone were associated with a stronger response to combined lures in males, and (iii) there was an indication that host-specialist male Lepidoptera responded more strongly to the combined lures than generalists. The properties of the plant volatile, in terms of blend complexity and chemical category, were significant factors for certain methods. Attractant volatiles had a stronger effect on male responses to sex pheromones in agricultural than in orchard habitats. Analysis of wind tunnel studies revealed that the combination of plant volatiles with sex pheromones increased female attraction at an early stage, but aided male attraction at the final approach stage (fig. 3).

Interactions between attractant plant volatiles and sex pheromones

A previous meta-analysis reported that attractant plant volatiles alone have a significant effect on insect herbivore captures, particularly in Lepidoptera, with stronger effects on females than males (Szendrei and Rodriguez-Saona, 2010). This is supported by a more recent study included in our meta-analysis (Judd *et al*., 2017a), albeit other studies reported similar responses of both sexes to attractant plant volatiles alone (Li *et al*., 2018; Kong *et al*., 2020). In contrast, sex pheromone lures are designed to be highly effective for males, but are typically ineffective for females. Our meta-analysis indicates that combined sex pheromone–plant volatile lures are more effective than pheromone-only lures at attracting both sexes, although captures continue to be dominated by males due to the potency of sex pheromones. However, our findings support those of individual studies which reported highly variable success in combining proposed attractant plant volatiles with sex pheromones to attract males (e.g. Meagher, 2001; Hu *et al*., 2013; Barros-Parada *et al*., 2018).

Attractant vs. repellent plant volatiles

Repellent plant volatiles were far less studied than attractants, with only four field-trapping studies included in our meta-analysis, compared with 27 studies on proposed attractants. Despite the limited research in this area, plant volatiles tested as repellents relatively consistently deterred males from sex pheromones, particularly in wind tunnel studies, in contrast to proposed attractants which had highly variable outcomes. A similar pattern has been reported for studies of the effects of plant volatiles alone on herbivorous insects (Szendrei and Rodriguez-Saona, 2010). Non-host plant volatiles can interfere with male attraction to females, and suppress female egg-laying (McNair *et al*., 2000; Jactel *et al*., 2011), demonstrating their potential application in push–pull strategies (McNair *et al*., 2000; Cook *et al*., 2007) or mating disruption (Wang *et al*., 2016). However, more field studies are needed, given the lack of overall significant effect (*P*-value = 0.062) in our meta-analysis.

Sex-specific differences

Females consistently responded more strongly than males to combined lures compared with sex pheromone-only lures, especially in field studies. This is perhaps unsurprising given the low effectiveness of sex pheromone lures on female attraction; the addition of plant volatiles to sex pheromone traps increased the proportion of females from ca. 5 to 10% relative to male captures. As such, a key advantage of combined plant volatile and sex pheromone lures is the potential to attract both female and male Lepidoptera, albeit males typically remain dominant. This could have applications in mass trapping or monitoring programmes where detecting females is advantageous. However, the number of field studies reporting data for female captures was limited (16, compared to 27 for males), and only four of these 16 specified that no females were captured. As such, the significant positive effect of combined attractant lures on female capture rates could be affected by reporting bias. Where combined lures do not capture females, this could be explained by the limited mobility of females in some species (Li *et al*., 2012a; Miluch *et al*., 2014) and the repellent effect of conspecific sex pheromone (Barnes *et al*., 1992; Weissling and Knight, 1996; Judd *et al*., 2017b), although this appears to vary among species (Jósvai *et al*., 2016; Judd *et al*., 2017a).

Relative dosage: less is more?

Our findings strongly corroborate previous reports from individual studies that higher concentrations of host plant volatile relative to sex pheromone can inhibit male Lepidopteran responses to sex pheromones (e.g. Hu *et al*., 2013; Yu *et al*., 2015; Xiang *et al*., 2019). This effect was significant even for the limited number of EAG studies, suggesting that the addition of host plant volatiles at high relative doses do not repel males, given that EAG responses do not differentiate between attractant and repellent effects, but instead interfere with the attraction effect of sex pheromones (Deisig *et al*., 2014). This response could potentially help males avoid heavily defoliated host plants. If the relative concentration of plant volatile is too low however, it might not have any observable effect (Varela *et al*., 2011; Barros-Parada *et al*., 2018). As such, there is likely to be an optimal ratio of plant volatile to sex pheromone, which will depend on the component chemicals and target species. Although the ratio of repellent plant volatile to sex pheromone was not included in this meta-analysis due to limited previous research, some evidence suggests that the effect could be simpler, with stronger repellent effects at higher relative doses of plant volatile (Jactel *et al*., 2011; Wang *et al*., 2016).

Similarly, the effect of relative plant volatile dose on female attraction could be simpler, for example, higher doses of pear ester can increase female capture rates (Knight *et al*., 2005; Mitchell *et al*., 2008).

Blend complexity: keep it simple?

Unexpectedly, the use of single plant volatiles with sex pheromones outperformed more complex plant volatile blends in terms of male capture rates in the field. Although a previous meta-analysis of plant volatile effects without sex pheromones found that blend complexity increased effectiveness (Szendrei and Rodriguez-Saona, 2010), our findings suggest that using complex blends with sex pheromones could increase the risk of plant volatiles interfering with male responses to sex pheromones, as discussed above. For instance, in the case of *Grapholita molesta*, the lowest doses of (*Z*)-3-hexenyl acetate and 1-undecanol increased male capture rates by approximately 4.8 and 3.1 times, respectively, compared with pheromone-only traps (Yu *et al*., 2015). However, when these two plant volatiles were combined, capture rates were only 2.4 times higher than the pheromone-only controls. The authors hypothesise that this decrease in effectiveness was due to interference among the plant volatile compounds.

Plant volatile categories

There were no consistent differences in the effect of plant volatile compound type on male responses to pheromones across laboratory and field studies. Our findings indicated that green leaf volatiles were associated with the strongest responses of males to sex pheromones in the field, and were the most commonly studied chemical category. In contrast, fruit volatiles (limited to pear ester) were associated with the strongest attractant effects in wind tunnel studies.

A wide variety of plant volatiles were reported in the literature. For example, 37 individual compounds were included in our meta-analysis of field-trapping studies, in addition to blends of multiple compounds. These were typically selected based on their identified presence in host plants or previous success in attracting the same or similar species. (*Z*)-3-hexenyl acetate was the most frequently studied plant volatile, appearing in nine of the 35 field-trapping studies, while pear ester and phenylacetaldehyde were tested in seven and six field studies, respectively. Other alcohols and aldehydes were also frequently studied, such as (*Z*)-3-hexen-1-ol and (*E*)-2-hexenal which were each tested as unblended volatiles in three field studies. The relationship between plant volatile and growth stage or condition of the host plant (e.g. defoliated or undefoliated) could also be relevant in determining their interactive effects with sex pheromones on Lepidoptera (Tang *et al*., 2012).

The variable effects of plant volatile categories are unsurprising given the diversity of compounds within each category, while their effects also depend on target species and background odour. For example, linalool enhanced the attraction of codling moth *C. pomonella*, but inhibited the attraction of tobacco cutworm *Spodoptera litura* Fabricius, to their respective sex pheromones (Yang *et al*., 2004; Fang *et al*., 2018). In addition, the effects of herbivore-induced plant volatiles on phytophagous insect behaviour may depend on their survival strategy, e.g. gregarious vs. solitary species (Guo and Wang, 2019). Therefore, understanding the host plant volatile profiles of the target insect species, and their attraction to damaged vs. healthy plants, may be important to assemble informed hypotheses for potential future lure development.

Influence of habitat and host specialism

The positive effects (either synergistic or additive) of adding plant volatiles to pheromone traps on male capture rates were higher in herbaceous-crop agriculture than in orchard habitats, despite a similar number of studies in the meta-analysis. This could be because in herbaceous crops, combined traps are often used to increase male captures (e.g. Li *et al*., 2012b; Miluch *et al*., 2014; Fang *et al*., 2018), while in orchard pest management, the aim is often to attract both sexes (e.g. Light, 2016; Knight *et al*., 2017; Mujica *et al*., 2018). Only four studies were available in forestry contexts, and whilst results were generally positive overall, but non-significant, only one of the studies reported female capture rates (Jósvai *et al*., 2016). Pheromone traps positioned within host plant tree species have been shown to capture significantly more males of a specialist Lepidoptera than those in suboptimal congeneric hosts (Williams and Jonusas, 2019), while single-species forest stands tend to be more susceptible to specialist pests than generalists (Jactel *et al*., 2021), indicating potential applications for attractant and repellent plant volatiles for host-specialist Lepidopteran tree pests.

Our hypothesis that males of host-specialist Lepidoptera species would exhibit stronger responses to plant volatiles than generalist species was tentatively supported across all three methods but was not statistically significant. As such, the use of plant volatiles to increase male capture rates in pheromone traps might be easier to achieve for host specialist species.

Other potential causes of heterogeneity

Although our analysis provides some insights into the lack of effect or unexpected repellent effects of proposed attractant plant volatiles on male Lepidoptera responses to sex pheromones, other potentially important variables could not be investigated due to insufficient data. Mating experience is one such variable that can influence Lepidopteran responses to sex pheromones and plant volatiles, because newly mated males can stop responding to sex pheromone and may also change their response to plant volatiles (Deisig *et al*., 2014). For example, green leaf volatiles of host plants increased the response of unmated but not mated diamondback moth *P. xylostella* males to sex pheromone in a wind tunnel experiment (Reddy and Guerrero, 2000). This factor could potentially confound field studies where mating experience is uncontrolled.

Weather conditions such as temperature, humidity, and wind speed are also likely to affect success of combining plant volatiles with sex pheromones, and could explain some of the discrepancy between wind tunnel and field-trapping results. For example, flight activity of moths is dependent on suitable temperatures and wind speeds, while wind speed also affects trapping area (Elkinton and Cardé, 1988; Schouest and Miller, 1994; Reardon *et al*., 2006).

The choice and dosage of sex pheromone can also be relevant, although studies have found conflicting evidence of how these factors interact with plant volatiles. Stronger attractant effects have been demonstrated for plant volatiles combined with less effective pheromones (Knight *et al*., 2014; Miluch *et al*., 2014; Sans *et al*., 2016; Borrero-Echeverry *et al*., 2018), and with pheromones at underdosed or overdosed concentrations (Schmidt-Büsser *et al*., 2009). However, other studies have found the reverse pattern, where host plant volatiles reduce male attraction to incomplete synthetic pheromones, but increase attraction to optimal pheromones (Sans *et al*., 2016; Borrero-Echeverry *et al*., 2018). It is likely that this interaction depends on the combination of pheromone and plant volatile and whether the plant volatile stimulates receptors for missing pheromone components or interferes with pheromone detection (Deisig *et al*., 2014; Miluch *et al*., 2014). Clearly, initial dosage and release rates of both sex pheromones and plant volatiles are likely to be important factors influencing trap efficacy.

Finally, the effect of plant volatiles on Lepidopteran responses to sex pheromone appears to depend on background odour, which can interfere with plant volatile lures when their components overlap (Cai *et al*., 2017). This perhaps might explain the contrasting results from field studies in different crop types, while findings from laboratory studies in controlled environments are often not corroborated by field studies (Deng *et al*., 2004; Tang *et al*., 2012; Li *et al*., 2012b; Miluch *et al*., 2014).

Conclusion

This meta-analytic review provides evidence that the addition of attractant plant volatiles to sex pheromone traps leads to higher captures rates of adult Lepidoptera. A key advantage of combined plant volatile-sex pheromone lures is the potential to develop trapping approaches that attract both sexes, which could improve early detection, monitoring, and mass trapping programmes. Although research on proposed repellent plant volatiles is limited, we found preliminary evidence of repellent effects on males towards sex pheromones, which presents opportunities to develop natural pest management strategies such as push-pull and mating disruption approaches.

However, effects of attractant plant volatiles on male responses to sex pheromones were highly variable, and in some cases resulted in unexpected repellent effects. We found evidence that this effect depends on factors such as relative concentrations of plant volatile to sex pheromone, category of plant volatile tested and blend complexity. Hence, our findings demonstrate the potential applications of both attractant and repellent plant volatiles in Lepidoptera pest management, but that careful consideration of attractant lures is critical to minimise interference of plant volatiles on male attraction to sex pheromones. In addition, further research, particularly field trials, is urgently needed to investigate repellent volatiles.

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