MINI REVIEW

A meta-analysis of insect pest behavioral manipulation with plant volatiles

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Abstract
Many insect pests utilize plant volatiles for host location and untangling the mechanisms of this process can provide tools for pest management. Numerous experimental results have been published on the effect of plant volatiles on insect pests. We used a meta-analysis to summarize this knowledge and to look for patterns. Our goal was to identify herbivore and plant traits that might explain the herbivores' behavioral response to plant volatiles in field applications. We scored a total of 374 unique plant volatile-insect herbivore interactions obtained from 34 published studies investigating 50 herbivore pest species. Attractants had a significant effect on insect herbivore abundance but repellents did not; this latter result could be a result of the comparatively small number of field studies that tested plant volatiles as repellents (3%). Females were significantly more attracted to plant volatile baits than males. The diet breadth of herbivores was independent of a behavioral response to plant volatiles, but more case studies show effects of volatiles on chewers, followed by wood-borers and sap-feeders. There are more demonstrations of attraction to plant volatiles in Lepidoptera than in Thysanoptera. The method of plant volatile application had a significant effect on herbivore abundance and increasing the number of chemicals in individual baits attracted more herbivores. The magnitude of the response of herbivores to plant volatiles in forest and agricultural habitats was similar. We explore consistent patterns and highlight areas needing research in using plant volatiles to manage insect pests.

Introduction

The release of plant volatiles into the environment mediates plant-insect interactions that can be beneficial or harmful to the plant. The importance of these volatiles for herbivorous insects has been recognized for over 40 years (Kennedy, 1965; Dethier, 1982; Visser, 1986; Bernays & Chapman, 1994; Bruce et al., 2005). Because a large number of insect pests utilize plant volatiles in host location (Metcalf & Metcalf, 1992), untangling the mechanisms of these interactions could eventually provide tools for pest management, in addition to improving our understanding of the behavioral responses of insect herbivores to plant volatiles (Rodriguez-Saona & Stelinski, 2009).

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Herbivores can be attracted or repelled by volatiles emitted from plants (Visser, 1986; Foster & Harris, 1997). For example, herbivores are attracted to plant volatiles to locate food or potential mates, and female herbivores may also use plant volatiles to select oviposition sites. Thus, females may have a stronger response to plant volatiles than males (Curtis & Clark, 1979; Hern & Dorn, 2004), and are likely to be affected by plant volatiles, such as those induced by herbivory, when searching for oviposition sites (De Moraes et al., 2001). This has motivated research on the development of attractants for monitoring female flight and population densities in agricultural systems (Jang & Light, 1996; Hern & Dorn, 1999; Toth et al., 2007). Plants can also emit volatiles that provide insects with information on the presence of non-hosts or harmful substances, and these repellent volatile chemicals can yield new methods for crop protection (Pickett et al., 2006).

Linking certain insect life-history characteristics, such as their feeding guild, taxonomic group, and feeding specialization with behavioral responses to plant volatiles could reveal some wide-ranging applicability of plant volatiles in pest-management strategies. Herbivore feeding generally increases volatile emissions in plants (Schoonhoven et al., 1998) and often induces the plant to release novel compounds that may serve as an indicator of damaged plants for the third trophic level (Dicke & Sabelis, 1988; Turlings et al., 1990). The volatile response of plants to herbivory varies depending on the herbivore's feeding guild. For example, chewing and stem boring herbivores induced a stronger volatile response in plants compared with sap feeding herbivores (Turlings et al., 1998). Thus, feeding guild and type of damage can alter the composition of plant volatiles, and ultimately the herbivore's response to host plant volatiles. There is also considerable temporal variation in plant volatile emissions (Dudareva et al., 2004). For example, several leaf volatiles induced by herbivory are emitted in greater quantities during the daytime and thus synchronize with the plant's photoperiod (Loughrin et al., 1994; Rodriguez-Saona et al., 2001; but see De Moraes et al., 2001). Therefore, insects foraging at night might be limited not only by the availability of visual cues but also by the detectability of certain chemical cues released from plants. This might be true for most nocturnal foragers, such as moths, but not for daytime foragers such as most beetles. As a consequence, we predict differences in the behavioral responses of insects to plant volatiles based on the insect's taxonomic group and this information could be utilized in management strategies.

Multiple theories have been put forward to explain the evolution of insect–plant relationships (reviewed in Jermy, 1984). Similarly, hypotheses have been generated to explain the evolutionary role and function of plant volatiles (Holopainen, 2004; Firn & Jones, 2006; Pichersky et al., 2006). Whatever the evolutionary role may be, it is plausible that plant volatiles and herbivores exert an effect on each other (Berenbaum & Zangerl, 2008). Intraspecific variation is the basis for selection and is ubiquitous both in plant volatiles (Degen et al., 2004), as well as in how herbivores respond to plant volatiles (Maeda et al., 2001). From a plant's perspective, emission of volatiles may be adaptive if their effects cause a behavioral change in the interacting herbivore that results in a fitness benefit for the plant. Therefore, we would expect that plant volatiles have evolved to minimize herbivore attack either directly, by repelling herbivores, or indirectly, by attracting the herbivore's natural enemies. On the other hand, there is now sufficient evidence that herbivores are able to adapt and respond positively to certain plant volatiles (Bruce et al., 2005). Such co-evolutionary interactions between the two

may have led to the production of increasingly complex plant volatile blends. Furthermore, herbivore capacity for host finding is likely to vary based on the level of feeding specialization (Schoonhoven et al., 1998) and as a result, we expect specialist and generalist herbivores to respond to plant volatiles differently. Compared with generalist herbivores, numerous specialists are able to counter plant defenses and can locate host plants against a background of non-hosts (Berenbaum & Zangerl, 1998; Macel & Vrieling, 2003; Nieminen et al., 2003). The selective pressures imposed by generalist and specialist herbivores may favor the diversification of plant volatiles, as plants attempt to avoid adapted specialists while maintaining defenses against polyphagous herbivores (Wink, 2003; Lankau, 2007).

Identifying the quantity and quality of volatiles involved in the interactions between herbivores and plants is a first step in developing strategies based on manipulating their host finding behavior. Determining the roles of different components in a volatile blend in herbivore responses to plants became possible when sophisticated equipment became available for the isolation and identification of volatiles from plants (Agelopoulos et al., 1999; Bruce et al., 2005). As a result, well-defined plant volatiles, alone or in combination, have been deployed in the behavioral manipulation of herbivores. Examples include lures manufactured to monitor insect pests (Light et al., 2001), spraying a plant to increase its attractiveness in trap cropping (Martel et al., 2005), or making a crop less attractive by the application of repellent plant volatiles (Pickett et al., 2006). Plant volatiles tend to be characterized by a few major along with several minor components and both of these groups can represent chemical compounds that range from unique to extremely ubiquitous (Visser, 1986; Dudareva et al., 2004; Niinemets et al., 2004). There may be a great deal of variation on how this information is perceived and translated to a behavioral response by insect herbivores. These processes ultimately determine the identity, amount, and number of volatile chemicals that should be used in artificial lures.

Agroecosystems are inherently different from natural ecosystems, partly because the plants grown in cultivation are the result of careful selection, breeding, and engineering. Cultivated plants are often selected to produce lower amounts of secondary chemicals, which makes them more desirable to humans and less attractive to herbivorous insects (such as cucurbitacins in cucumber; Schoonhoven et al., 1998). Furthermore, cultivated plants are usually nourished differently than a plant growing in the wild, which could lead to different patterns of allocation and ultimately quantitative and qualitative differences in the chemicals released, and thus a novel selection pressure on

herbivores. From the herbivores' perspective, finding a host plant is expected to differ depending on the availability of a resource, and thus the degree of plant apparency in forest and agroecosystems may influence volatile emissions in plants.

We used a meta-analysis to test for factors that may influence the attraction and repellency of insect herbivores to plant volatiles focusing on the role of plant volatiles in practical applications for pest control. This type of analysis combines the results from numerous published studies, most commonly through a standardized measure of effect size, which provides a more objective and informative alternative to classical 'vote-counting' literature reviews (Osenberg et al., 1999). Our goal was to detect general patterns based on different insect and plant traits that might explain the behavioral reaction of herbivores to plant volatiles applied in the field. We addressed the following specific questions: Are insect herbivore responses to plant volatiles influenced by gender, feeding guild, taxonomic group, and diet breadth? Does blend complexity (i.e., number of plant volatile compounds) affect insect attraction? Are there differential effects on attraction based on the type of chemical compound (i.e., chemical class)? Are there differences in the success of plant volatile applications in pest-management based on certain plant attributes such as taxonomic group or degree of cultivation?

The database and meta-analysis

Studies aimed at assessing the effects of plant volatiles on insect pests in field situations were found by conducting searches on the 'Web of Science' (ISI) electronic bibliography database (1984–2008). We used the search terms 'field', 'plant volatile', 'pest', and 'management' in different combinations and restricted the search to the following subject areas: entomology, ecology, horticulture, agronomy, and forestry. In addition, we surveyed the literature cited in papers to find studies that met our criteria. We selected studies that reported on the behavioral effect of chemically definable plant volatiles (individually or in blends) on herbivore species tested under field conditions. We did not include studies that examined the effect of combinations of plant volatiles with insect-derived volatiles. Typically, experiments involved placing dispensers with synthetic odors in replicated field plots and then counting insects on traps. We only included studies that had a control treatment, clearly reported means, a measure of variance (e.g., standard error of the mean or standard deviation) and sample size for both control and treatment groups. We scored a total of 374 unique plant volatile-insect interactions obtained from 34 published studies investigating 50 insect herbivore species (Appendix S1).

The measured variable was in all cases herbivore abundance (i.e., the number of herbivores). Each unique plant volatile–herbivore combination was considered an individual observation, thus only one effect size was calculated for any given combination of plant volatile treatment and herbivore. This unit of replication is justified given the biologic reality that different herbivore species often respond differently to plant volatiles (Cardé & Bell, 1995).

A positive effect size indicates that a greater level of herbivore abundance was observed in the presence of plant volatile(s), whereas a negative effect size denotes a repellent effect in the presence of a plant volatile. An effect size near zero suggests that plant volatiles had little-to-no impact on focal herbivores. We used Hedges' d statistic to score effect sizes, because this measure of effect size has been routinely used in ecological meta-analyzes (e.g., Langellotto & Denno, 2004; Kaplan & Denno, 2007), and consequently can be easily interpreted by scientists. In cases where herbivores were repeatedly sampled at multiple times within a given season we only used the date when herbivores were at peak abundance. If the same treatment was repeated over multiple years or at different sites, a separate meta-analysis was conducted to attain an overall effect size over years or sites.

The statistical program METAWIN 2.0 (Sinaur Associates, Sunderland, MA) was used for scoring effect sizes and conducting the analysis (Rosenberg et al., 2000). Mixed-effects models were used throughout our analyses and, initially, we used a model with no data structure to determine the cumulative effect size and the degree of heterogeneity among all observations in our dataset. To account for the violation of basic distributional assumptions that may occur with meta-analytical data, re-sampling tests (999 iterations) were performed to generate cumulative effect sizes with 95% bootstrap confidence intervals (CI) (Gurevitch & Hedges, 1999). We used a more conservative $\alpha = 0.01$ as our basis of determining significant differences to account for the problem of committing Type-1 errors with multiple comparisons. In addition, to address the 'file-drawer' problem whereby non-significant effects are less likely to be published, we used Rosenthal's Method ($\alpha = 0.05$) to calculate a fail-safe value. This method estimates the number of non-significant observations that would need to be added to our dataset to change the outcome of the analysis from significant to non-significant (Rosenberg et al., 2000).
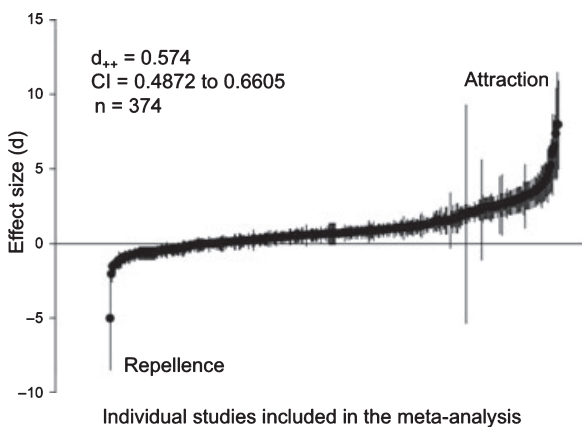
Next we used a categorical model to compare effect sizes using plant, volatile, and herbivore traits as predictor variables and effect sizes for herbivore abundance as response variables. For each category, a mean effect size (d_+) was calculated and reported with 95% bootstrap CI. Effects are considered statistically significant if CI do not bracket zero.

Between-group heterogeneity (Q_B) was tested against a chi-square distribution to determine whether significant differences existed among groups of predictor variables. Groups with fewer than five observations were excluded from the categorical analyses.

We conducted categorical data analysis focusing on: herbivore sex, herbivore feeding guild, herbivore taxonomic group, herbivore diet breadth, the volatile release device, the number of plant chemicals used as a single treatment, and type of chemical compound (chemical class). Herbivore diet breadth was scored as monophagous (feeding on one species of plant), oligophagous (feeding on multiple species within one plant family), or polyphagous (feeding across multiple plant families). We scored the herbivores' feeding guild as leaf-chewer, sap-feeder, or wood-borer. We also investigated the difference between plant volatile effects in agricultural vs. forestry systems.
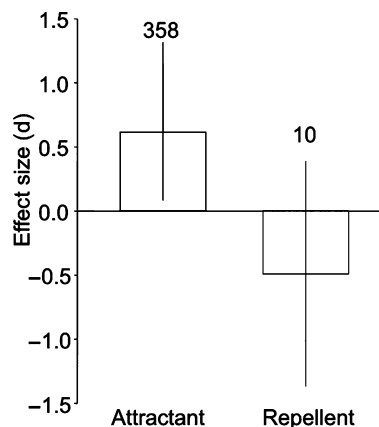
Attractants and repellents

The results of the meta-analysis provided evidence for the attraction of herbivores by plant volatiles in 76% of all interactions (286 of 374) in our dataset. The cumulative effect size for herbivore abundance was significantly >0 with a CI that did not bracket zero ($d_{++} = 0.574$, CI: 0.4872–0.6605), but the magnitude of the effect size varied greatly (Figure 1). This result should be considered robust given the large number of non-significant observations that would need to be added to our database to change the outcome of this analysis (i.e., the fail-safe value for herbi-

vore abundance was 74 071.8). An effect size of 0.2 is considered small, 0.5 moderate, and 0.8 large (Cohen, 1988); consequently, plant volatile effects on herbivore abundance was intermediate according to the mean effect size. We detected significant heterogeneity in effect sizes for herbivore abundance ($Q_T = 1 108.5$, P<0.01; n = 374, where Q_T describes total heterogeneity in effect sizes). This indicates that the variation among effect sizes is greater than expected based on sampling error and suggests that additional factors should be investigated as potential explanatory variables (Rosenberg et al., 2000); we therefore proceeded to evaluate the importance of various traits.

Most studies in the meta-analysis hypothesized and determined the behavioral effect of plant volatiles (attractant vs. repellent), and based on these results we compared the effect sizes between these two groups. Only 3% of the studies tested plant volatiles as repellents, and 60% of these used monoterpenes in forest ecosystems. This may mean that it is easier and perhaps more effective to use plant volatiles as attractants in the field, or that field application of plant volatiles as repellents is under-explored (but see Pickett et al., 2006; Turlings & Ton, 2006). As expected, a significant difference was observed ($Q_B = 59.18$, P<0.01; Figure 2) between attractants and repellents, but the repellent effect CI bracketed zero indicating that this effect was not significantly different from expected. On the other hand, attraction was significantly different from zero, i.e., the available literature demonstrates significant attraction but not repellent effects of plant volatiles.

Figure 1 The distribution of effect sizes across all studies measuring the effect of plant volatiles on insect herbivore abundance in field experiments (error bars represent variance). Effect sizes below zero indicate repellence, whereas effect sizes above zero indicate attraction. The cumulative effect size (d_{++}) for herbivore abundance was significantly >0 with a confidence interval that did not bracket zero.

Figure 2 Insect herbivore behavioral response to plant volatiles in field experiments. Error bars represent 95% bootstrap confidence intervals. Numbers above error bars represent the no. observations used to calculate effect sizes in each category. Confidence intervals overlapping zero denote non-significant effect sizes.

Sources of variation in insect attraction to plant volatiles

Males and females

The response to chemicals in the environment is often different between female and male insects (Natale et al., 2003). Response to plant volatiles may not be as markedly different between the sexes as the response to pheromones, but differences in host plant use are expected based on the roles plants play in insect reproduction. A potential explanation for this is that if oviposition sites are associated with the host plant, there is an additional evolutionary advantage for the female insect to be able to recognize host odors. For example, some female moths have specific olfactory receptor neurons for plant odors that replace pheromone sensitive ones present in males (Heinbockel & Kaissling, 1996; King et al., 2000). This physiological difference may translate into an increased attraction to plant volatiles for females. From the meta-analysis, we found that females were significantly more attracted to baits with plant volatiles than males ($Q_B = 26.68$, P<0.01; Figure 3A). Management methods targeting the removal of females from the population have a greater impact on reproduction than removal of males; therefore, female attractants are particularly valuable pest-management tools. When targeting females for behavioral manipulation with plant volatiles, it is essential to understand how factors such as mating status, age, and hunger level may change the level of attractiveness of females to artificial baits (Cornelius et al., 2001).

Feeding guilds

Our results suggest that insect herbivores with different modes of feeding (i.e., feeding guild) respond differently to plant volatiles. A significant difference in effect size among the feeding guilds ($Q_B = 23.71$, P<0.01; Figure 3B) indicates that more case studies show attraction of chewers to plant volatiles, followed by wood-borers, with the least number of cases for sap-feeders. This could be the result of differential attraction of herbivores with different feeding modes to plant volatiles. Turlings et al. (1998) found that chewing insect damage consistently produces higher levels of volatiles than damage by a borer or a sap-feeder. They suggested that increasing mechanical cell damage during feeding is positively related to the amount of volatiles emitted by the damaged plant. This taken together with our results may mean that chewers, the group that induces plants to produce copious amounts of volatiles, are also more receptive and responsive to plant volatiles when they are used in baits.

Taxonomy

Insect taxonomy was a significant factor in determining the effect size of the positive response to plant volatiles ($Q_B = 41.92$, P<0.01; Figure 3C). Thysanoptera were the least attracted and Lepidoptera were the most attracted to plant volatiles in the field, with Coleoptera falling between the other two taxonomic groups. This outcome may be a result of fundamental life-history differences among the examined insect orders, specifically regarding movement, odor perception, and thus orientation to odors. Encounter rates with a stationary object such as a baited trap are more frequent in case of good flyers such as many adult Lepidoptera, which could account for the success in using plant volatile baited traps with this group. These results need to be re-examined in more detail when more studies are available covering a wider range of taxonomic units.

Figure 3 Effect of plant volatiles on insect herbivore abundance in field experiments based on herbivore (A) sex, (B) feeding guild, (C) taxonomic grouping, and (D) diet breadth. Error bars represent 95% bootstrap confidence intervals. Numbers above error bars represent the no. observations used to calculate effect sizes in each category. Confidence intervals overlapping zero denote non-significant effect sizes.
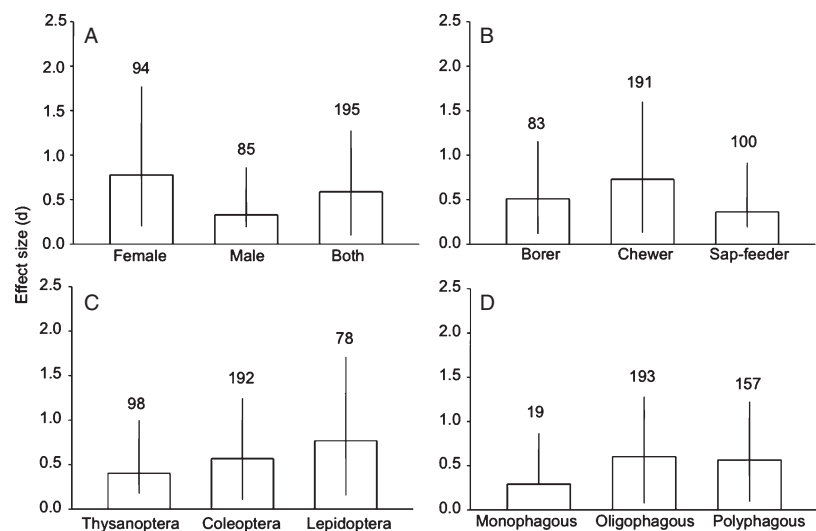
Diet breadth

The diet breadth of herbivores may determine the outcome of the behavioral response to plant volatiles; however, in the meta-analysis we did not find overwhelming evidence for this ($Q_B = 4.87$, $P = 0.08$; Figure 3D). There are examples of specialists that use specific plant chemicals to locate host plants (Hern & Dorn, 2004), but host plant finding seems more often to involve mixtures of chemicals that are common to many plants (Visser & Avé, 1978; de Bruyne & Baker, 2008; Webster et al., 2008). The large variety and variability of volatile chemicals emitted by plants favors robust and adaptable herbivore sensory systems as opposed to highly specialized ones. Although the specialization of receptor neurons is infrequent, the behavioral responses tend to differ based on even the slightest differences in odor blends (Bruce et al., 2005). The relatively prevalent phenomenon in insects of a generic receptor system combined with a highly variable behavioral response to specific blends means that using plant volatiles effectively in pest management requires detailed understanding of insect chemical ecology.

Mode of deployment

Regarding the differences between the modes of plant volatile deployment in the field, we observed a significant effect ($Q_B = 95.72$, $P<0.01$; Figure 4A) among the tested groups, with spray application having a non-significant negative effect and the other applications a positive effect on herbivore abundance (i.e., attraction). Plant volatiles generally need to be applied in larger volumes than pheromones, because they have to compete with a multitude of background odors. In addition, the smaller molecular weight compounds tend to be more volatile and these tend to be

more important in affecting insects at large distances (Bernays & Chapman, 1994). This means that the small holding devices traditionally available for pheromone field applications are not always adequate and cannot be readily adapted for plant volatiles. Vials, both plastic and glass, were frequently used in the studies included in the meta-analysis, but unless the vials are made of a permeable material, it is difficult to standardize release rates among vials and to prevent swift evaporation. Standardizing release rates is not only problematic because of the type of device, but also because of the differences between functional groups and chain-lengths among compounds. Spraying on the crop could provide a solution to the volume problem, but other issues such as rain-fastness and evaporation may make it less practical. In the studies we examined in the meta-analysis spraying application was often associated with repellents, whereas attractants were frequently deployed in vials. The lack of an observed effect in the repellent literature and the effect observed in the attractant literature may be the consequence of the differences in release devices. It is clear from our literature survey that more experimenting to develop better-suited and standardized release technologies is much needed in plant volatile deployment.

Blend complexity

The question whether a single compound is sufficient to attract insect herbivores or a mixture of compounds is required is of particular interest when plant volatiles are deployed. Mixtures can be perceived by insects in a manner that is qualitatively different from the perception of compounds applied singly (Piñero et al., 2008). Thus, we were interested whether the number of chemicals used in a
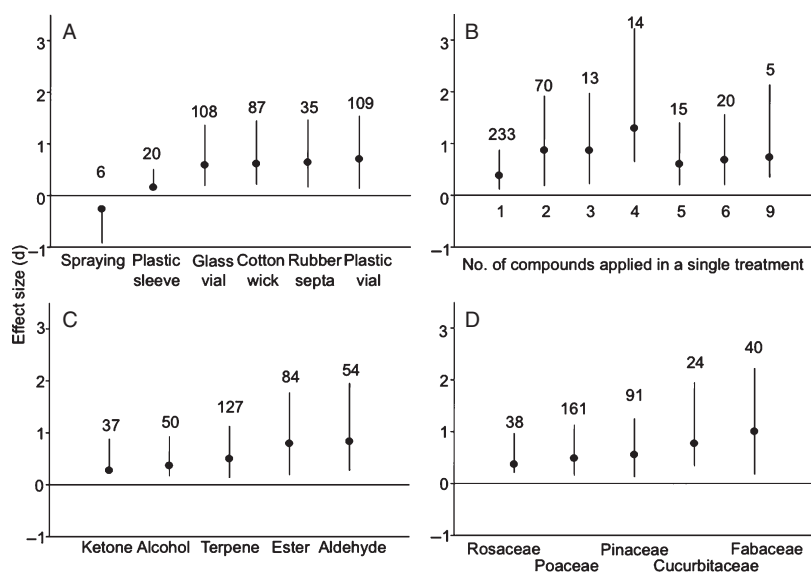
Figure 4 Effect of plant volatiles on insect herbivore abundance in field experiments based on (A) mode of application, (B) no. chemicals in an individual plant volatile treatment, (C) chemical class, and (D) plant family. Error bars represent 95% bootstrap confidence intervals. Numbers above error bars represent the no. observations used to calculate effect sizes in each category. Confidence intervals overlapping zero denote non-significant effect sizes.

single treatment affected herbivore abundance, and we detected a significant effect ($Q_B = 68.84$, $P<0.01$; Figure 4B), with increasing number of chemicals in a blend attracting more herbivores. Manufacturing artificial plant odor blends is complicated in part because of the high variability involved both in what plants produce and how the insects detect and respond to this information. Our current understanding of the process of host plant odor recognition suggests that blends are likely to yield better results in baits than single compounds (Visser, 1986; Bruce et al., 2005). We hypothesize that the result of the meta-analysis is because increasing the number of volatiles in a blend is more likely to include compounds that serve as key cues for the insect (sampling effect), but creating realistic and effective ratios is a more formidable task as the number of components and their possible permutations increase (complementary effect). Because of the complementary effect, the more complicated baits may also be less potent as their development requires a substantial amount of prior knowledge of insect behavior and physiology, as well as plant chemistry.

Type of chemicals

We detected a significant effect of chemical class ($Q_B = 54.18$, $P<0.01$; Figure 4C). Field use of plant baits requires that the chemicals used in the bait are easy and relatively cheap to manufacture and these factors increase bias toward those chemicals that meet the above requirements. Aldehydes were the most effective group of attractants when used in plant baits according to our results (Figure 4C); among aldehydes, phenyl acetaldehyde was used in 65% of the examined studies. Blends of six carbon aldehydes and alcohols, collectively called green leaf volatiles, are released both constitutively and induced upon wounding; these compounds are highly volatile, ubiquitous in plants, and detectable by a diverse group of insects both specialist and generalist (Schoonhoven et al., 1998; Arimura et al., 2005). For example, the 'right' blend of green leaf volatiles is important to *Leptinotarsa decemlineata* (Say) in orienting to the host (Visser & Avé, 1978), and specific green leaf volatiles coupled with insect pheromones have yielded great successes in behavioral manipulation of some coleopteran and lepidopteran pest species (Reddy & Guerrero, 2004). Although high volatility of green leaf volatiles may make them more likely to be detected by insect antennae and therefore a better candidate for behavioral manipulation, this chemical property may also hinder field applications because of a rapid loss of product in the deployment vessel. Among terpenes, 70% of monoterpenes were used in studies in forest ecosystems; these compounds are the most important volatile compounds emitted by boreal forests, with the strength of emission depending on the tree species (Spracklen et al., 2008). Single plant species can emit more than 20 types of monoterpenes and although biochemical regulation of most plant volatiles is assumed to be fast, maximum monoterpene emissions are reached several hours after illumination (Niinemets et al., 2004). Terpenes are the largest class of plant secondary metabolites and investigation of this group of chemicals is an active area of plant volatile research (Dudareva et al., 2004).

Plant taxonomy

A comparison of plant taxonomy at the family level showed significant effects of herbivore abundance, with the greatest attraction in Fabaceae (Figure 4D). There is ample evidence that plants in different taxonomic groups emit qualitatively and quantitatively different volatiles. For example, Schoonhoven et al. (1998) following a literature survey pointed out that: legumes (Fabaceae), rosaceous species, and maize (Poaceae) emit large quantities of alcohols and aldehydes in their headspace.

Chewing insects were commonly associated with alcohols, aldehydes, esters, and terpenes, whereas borers were typically associated with terpenes. Esters and ketones were frequently used in baits targeting sap-feeders (Figure 5).

Management methods

In agricultural systems, two mechanisms exist to improve the protection of plants from herbivory through the application of plant volatiles: breeding/engineering plants whose volatile blends attract fewer herbivores and/or more natural enemies, or isolating chemicals and deploying them in a variety of applications and formulations. However, in forestry, frequently only the latter option exists. The magnitude of positive response of herbivores to plant volatiles in forestry vs. agricultural habitats was not statistically different ($Q_B = 0.11$, $P = 0.75$; Figure 6). This finding reflects the similarity in the relative success of the programs that use plant volatiles to monitor or manage insect populations in either type of habitats.
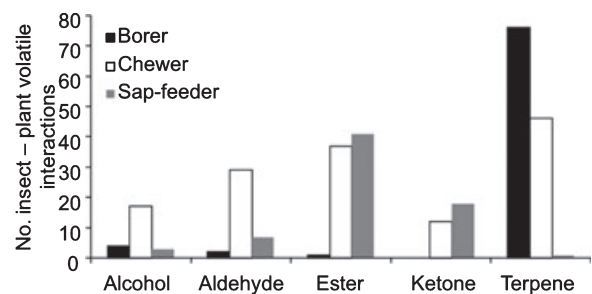
Figure 5 The relationship between insect herbivore feeding guild and chemical class in field experiments. Data represent the frequency of studies included in the meta-analysis.
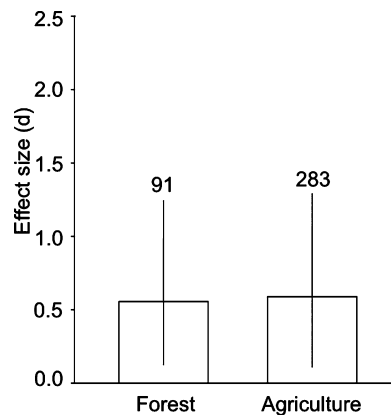
Figure 6 Influence of habitat type on the response of insect herbivores to plant volatiles in field experiments. Error bars represent 95% bootstrap confidence intervals (CI). Numbers above error bars represent the no. observations used to calculate the effect sizes in each category. Confidence intervals overlapping zero denote non-significant effect sizes.

Conclusion

The current study is the first to provide an overview of the current achievements and challenges of applying plant volatiles in pest management. Some of our results can be used to guide development of plant volatile bait manufacturing. Our investigation of the literature has led us to point out areas that are lacking and require further research, such as need for novel modes of application and perfecting ratios of blends vs. testing individual volatile components.

For plant volatiles to be used effectively in pest management, first we need to understand how particular plant processes and herbivore behaviors may influence a specific system, and secondly we need to summarise our knowledge to recognize patterns in the accumulated data. For that reason, some of the generalizations provided in this study might not apply to all plant-insect interactions; however, our findings will serve as a valuable foundation for comparison of future studies with patterns we detected in the available literature. There is a wealth of valuable published studies that report on laboratory results of interactions between plant volatiles and insects. We would like to encourage these efforts to continue their transition into field experiments, which are the fundamental precursors for developing practical solutions for pest management.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix 1 List of studies used in the meta-analysis.

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