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**Semiochemicals for thrips and their use in pest management**

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Abstract

Thrips (Thysanoptera) are small insects that can cause huge problems in agriculture, horticulture and forestry through feeding and the transmission of plant viruses. They produce a rich chemical diversity of pheromones and allomones and also respond to a broad range of semiochemicals from plants. These semiochemicals offer many opportunities to develop new approaches to pest management. Aggregation pheromones and plant-derived semiochemicals are already available in commercial products. We review these semiochemicals and consider how we can move away from their use mainly for monitoring to their use for control. We still know very little about the behavioral responses to semiochemicals and we identify that research in this area is needed to improve the use of semiochemicals in pest management. We also propose that thrips should be used as a model system for semiochemical responses of small insects that have limited ability to fly upwind.

# INTRODUCTION

Thrips (Thysanoptera) are small insects that are very common, but easily overlooked. Of the 6,000 known species, over a hundred are plant pests in agriculture, horticulture and forestry, causing damage by feeding and transmission of plant viruses (71, 103). Several are invasive pests and a few are of international quarantine concern (25, 55, 137). They are notoriously difficult to control, partly because they develop insecticide resistance very quickly (25, 39, 99). The western flower thrips (WFT) (*Frankliniella occidentalis*) and the onion thrips (OT) (*Thrips tabaci*) are major worldwide pests, causing billions of dollars of damage (25). We urgently need novel approaches to thrips pest management that provide alternatives to synthetic insecticides (31, 99). Research on thrips semiochemicals could provide these new approaches.

There has been much research on the semiochemicals of larger insect pests, such as moths and beetles, but much less on the very many smaller insect pests, such as thrips. These have limited ability to fly upwind and their responses to semiochemicals do not fit the classic model of upwind anemotaxis found in moths (15). Not enough is known about the responses of flying thrips to semiochemicals to classify them easily into standard terms, such as ‘attractant’ or ‘arrestant’, and in many cases these would be misleading because of the critical interaction with visual stimuli. The terminological problems of describing semiochemicals are discussed elsewhere (83).

Supplemental Tables 1, 2 and 3 provide comprehensive lists of thrips species and the semiochemicals that they produce or that affect them. Supplemental Table 4 lists beneficial arthropods that are affected by thrips semiochemicals.

# SEMIOCHEMICALS PRODUCED BY THRIPS

## Aggregation Pheromone

Some species of thrips form male aggregations for mating (51, 84, 89, 120, 139), and these appear to be mediated by aggregation pheromones. Experiments with volatiles from live insects have shown that adult males and females respond to the odor from adult males, but not to the odor of adult females (3, 54, 91, 143). In some cases, only females respond (26, 84). The aggregations sometimes form at particular times of day (120, 139), and the release rate and ratio of pheromone components can also change with time of day (74).

The compounds in the male-produced aggregation pheromone have been identified for five thrips species (Table 1) and all attract both males and females. Where two compounds have been identified, one compound is consistently released at a higher release rate than the other, so they are here referred to as the major and minor compounds respectively. The compounds are all terpenoid esters or monoterpene alcohols and most are chiral. The major compounds are less volatile than the minor compounds, for example the WFT major compound, neryl (*S*)-2-methylbutanoate, has a boiling point of about 340°C while the minor compound, (*R*)-lavandulyl acetate, has a boiling point of about 230°C (at atmospheric pressure), which means that a particular dose ratio (by mass) in a dispenser is unlikely to give the same ratio for the release rate of the volatiles.

In many species, adult males have sternal pore plates on the underside of the abdomen (86), which have large amounts of glandular tissue underneath and pores connecting the tissue with the exterior (35, 65, 85, 110), strongly suggesting that the glands produce and release pheromone. These glands were initially thought to be the source of the male-produced aggregation pheromone (43), but the more recent discovery of aggregation pheromones in *Megalurothrips sjostedti* and *M. usitatus*, which have little or no sternal gland material (65), casts doubt on this.

Investigations of the roles of the major and minor compounds have given inconsistent results. WFT and *F. intonsa* share the same two compounds (Table 1), but each species can still distinguish males of their own species in a Y-tube olfactometer (72, 144). Research in China found that the major:minor ratio of release rates, measured by SPME (solid-phase microextraction), was about 13:1 in WFT and 2:1 in *F. intonsa* (144). However, in the UK, measurements with SPME gave ratios for WFT ranging from 5:1 to 0.8:1 (43). Field experiments in China with traps baited with dose ratios of 8:1 and 4:1 showed a differential response to ratio, with 8:1 catching more WFT and 4:1 catching more *F. intonsa* (72). In contrast, field trials for WFT in Spain with dispensers calibrated for release rate gave similar catch increases with release rate ratios ranging from 50:1 to 1:1, but the major compound alone caught most, giving no evidence for synergy (105). In Spain, the addition of the minor compound either gave no increase relative to the major compound alone or decreased trap catch (43, 105). For this reason, commercial pheromone products for WFT (see below) include only the major compound. The role of the minor compound needs further study.

Trapping experiments to test thrips pheromones usually use blue or yellow sticky traps, which are visually attractive to flying adults, and the trap catch increase, as a ratio of treatment catch to control catch (T:C), ranges from about ×1.5 to ×4 for the major compound of WFT (13, 41, 106, 107). When less attractive trap colors are used, the T:C ratio increases, but far fewer are caught (106), indicating that the landing response involves an integration of olfactory and visual responses.

Besides increasing trap catches, the aggregation pheromone compounds have other behavioral effects, such as increasing walking activity, even at very low concentrations (93), and these are poorly understood.

## Cuticular Hydrocarbons and Contact Pheromone

Cuticular hydrocarbons have been studied so far only in WFT (94). The profile from adults consisted of a mixture of *n*-alkanes and branched monomethyl and dimethyl alkanes. Adult males had large amounts of 7-methyltricosane, whereas only trace amounts were found on females. Bioassays from this study showed that it was a contact pheromone (94). It could be used for species recognition or substrate marking or as an antiaphrodisiac pheromone (4, 94).

## Antiaphrodisiac Pheromone

In the poinsettia thrips (*Echinothrips americanus*), females typically mate only once. Krueger et al. (64) found that an antiaphrodisiac pheromone, dimethyl adipate, is produced by adult males and transferred to females during mating. Dimethyl glutarate was also found on males, but not detected on females, perhaps because it was below the limit of detection. Subsequent males ignored females that were marked with either compound. However, details of the exact roles of the two compounds are yet to be established; they could have other functions (64). Antiaphrodisiac pheromones may well be present in other species, including WFT (4).

## Alarm Pheromone

In many species of thrips, adults and larvae produce a droplet from the anus when disturbed or threatened. Often the droplet is placed on the attacker (45), which suggests that it is used as a defensive allomone (see below). However, such droplets could also function as alarm pheromones, particularly where related thrips are close together, such as in galls. Although many components of anal droplets have been identified, few have been tested for an alarm pheromone function. Perillene has been implicated as an alarm pheromone in several genera in the sub-family Phlaeothripinae of the family Phlaeothripidae (114). The compounds known or assumed to function as an alarm pheromone are listed by thrips species in Supplemental Table 1.

In WFT, threatened larvae produce a droplet from the anus, consisting of decyl acetate and dodecyl acetate in water, with the volume and ratio varying with larval age and level of danger (24, 78, 118). The compounds are described as an alarm pheromone (118), but they have many effects. Exposed larvae walk away from the source, produce an anal droplet, increase vigilance and drop from leaves, whereas exposed adults walk away from the source, take off more readily, land less readily and lay fewer eggs (23, 77, 118). This illustrates how thrips pheromones can have many effects and we should be cautious about assuming single roles for thrips-produced compounds. Both pheromone compounds are active and no synergy has been detected (76, 118).

## Other Pheromones

In WFT, seven pheromone compounds with a wide range of functions have been identified so far (Supplemental Table 1) and it is likely that more compounds and functions will be discovered. For example, observations suggest the possibility of a volatile mating pheromone (93). Many other thrips species have obvious pheromone production sites, such as sternal pore plates (86), suggesting that pheromones are widespread, and observations of anal droplets in other species (7) suggest that many may produce alarm pheromones. A female-specific compound has been detected in adult and immature *E. americanus*, which may be a novel pheromone (66). The sub-social and social species of thrips in the family Phlaeothripidae may well yield pheromones mediating social interactions. For example, the foraging behavior of a species that lives in colonies on tree trunks indicates the use of a trail pheromone (50).

## Allomones

Very many thrips species produce an anal droplet when threatened (see above), and the behavior may be widespread in the Thysanoptera. The droplets are often placed or wiped on the attacker by bending the abdomen, and long setae at the end of the abdomen act like a paintbrush to help spread the droplet (45, 46). Species in the family Phlaeothripidae have a characteristic tubular structure at the end of the abdomen, which can be articulated and allows accurate placement of the droplet (45).

The droplets have been particularly studied in the family Phlaeothripidae (Supplemental Table 1). The larger of the two sub-families, Phlaeothripinae, contains about 3,000 species, which mainly feed on leaves, flowers and fungi, and includes many gall-forming species and some that show social behavior (132). The composition of phlaeothripine droplets is species-specific and presents a rich chemical diversity, including alkanes, alkenes, saturated and unsaturated carboxylic acids, esters, monoterpenes, monoterpenoids, quinones, pyranones and aromatic compounds (11, 116). Some droplets contain single compounds. For example, the flower-inhabiting thrips *Haplothrips leucanthemi* produces droplets containing about 25 ng of a C10 lactone (mellein) (12), and the gregarious leaf-feeding thrips *Bagnalliella yuccae* produces droplets containing another C10 lactone (γ-decalactone) (45). Other species have droplets containing many diverse compounds, for example, both *Leeuwenia pasanii* and *Suocerathrips linguis* have 11 compounds in their droplets, but only one compound (a C17 alkane) in common (40, 116). The abundance and diversity of compounds in single droplets raises questions about why so many are needed and what functions they all have.

Defense against predators has been demonstrated against many ant species. When in contact with a droplet or synthetic components of droplets, ants can be repelled (12, 45, 116, 133), deterred (45) or incapacitated in various ways. For example, little fire ants (*Wasmannia auropunctata*) in contact with droplets from *Gynaikothrips ficorum* dragged themselves along the substrate with the legs extended for several minutes and were sometimes attacked by other worker ants (46). A pyranone compound in the droplets of three *Holothrips* species caused paralysis and mortality at high doses in the ant *Formica japonica* (116). The effects on other predators, such as mites and bugs, have not been tested in phlaeothripines.

While some components of droplets are active against ants or may have a role as alarm pheromones (see above), other compounds may be solvents. For example, in some phlaeothripines, solid acetates or quinones are dissolved in liquid long-chain alkanes and acetates (40, 113). A biosynthetic pathway for the many acetates, alkanes and alkenes, including those with unusual terminal double bonds, has been proposed for *Suocerathrips linguis* (40). The acetates and hydrocarbons may also act as surfactants, so that droplets spread out and coat attackers rapidly with a long-lasting coating (40, 133).

The use of defensive droplets may be important for allowing some thrips species to maintain large colonies (45). Gall-inhabiting species often live in large colonies and such species commonly produce monoterpenes and monoterpenoids in their droplets (116). Some of these compounds have anti-fungal properties, which may protect galls from fungal infection (116).

The smaller sub-family, Idolothripinae, contains about 700 species, which feed on fungal spores, with some showing sub-social behavior (132). Idolothripine droplets are less chemically diverse and usually consist of juglone (5-hydroxy-1,4-naphthalenedione) and from two to nine C10 to C14 carboxylic acids (115) (Supplemental Table 1). The compounds are found in both adults and larvae (115). Juglone is a potent ant repellent (113). Although the long-chain acids may also be repellents, they could be solvents, stabilisers or aids to coating predators (115).

Anal droplets have been investigated for very few species in the family Thripidae, despite the large number of pest species in the family. Larvae in a few species in the sub-family Panchaetothripinae carry around a droplet on the end of the upturned abdomen. For example, larvae of *Caliothrips fasciatus* carry a drop of red liquid that is used in defense against parasitoid wasps (104). The anal droplets produced by larvae of WFT function as an alarm pheromone (see above), but they also deter attacking predators (23). Larvae of OT produce an anal droplet when threatened, which makes predatory mites withdraw and groom (7), but the contents have not been identified. Anal droplets may well be widespread in the Thripidae and may have many functions. The apparent absence of anal droplets in adult thripids may be because they often live in habitats where adults can fly away easily.

Anal droplets have been analysed in relatively few of the 6,000 or so species of Thysanoptera. Useful ant repellents and antibiotics may await discovery.

# SEMIOCHEMICALS PRODUCED BY PLANTS

## Arrestants, attractants and lures

Non-pheromone semiochemicals (e.g. kairomones or synomones) or their mimics, as lures, provide an alternative to pheromones, as these compounds can be very powerful. For example, ethyl nicotinate increases trap catch by more than ×100 for *Thrips obscuratus* (96), and methyl anthranilate increases trap catch by more than ×500 for *Thrips hawaiiensis* (47). Additionally, non-pheromone semiochemicals can trap more than one species of thrips, can trap both males and females (58), and the active ingredients are often commonly available and relatively inexpensive.

The multiple studies of walking thrips and their directional response to compounds in olfactometers (Supplemental Table 2) indicate that walking thrips use chemotaxis, so these compounds appear to be attractants (28). For flying thrips, the behavioral response is likely to be more complex, reflecting the many plant cues (color, odor, shape etc.) and the limited ability of thrips to fly upwind (128). Kirk (52) proposed an odor-induced visual response for thrips, which is still most consistent with the evidence to date , but it is a mechanism not well recognised in the insect semiochemical literature. Multiple studies have associated non-pheromone semiochemicals with decreased flight activity (9, 111, 128). These semiochemicals have also increased take-off activity (135), but in quite different experimental designs. The behavioral response is important for both testing and utilisation of odors for trapping (see below). Given the lack of knowledge about the behavioral responses of flying thrips, we feel that use of the term ‘attractant’ *sensu stricto* (28) for compounds that increase trap catch is not justified.

Compounds. Supplemental Table 2 provides a comprehensive list of non-pheromone compounds that have been reported to attract thrips in laboratory assays or to increase thrips trap capture in the field (henceforth referred to as lures). The range of compounds primarily reflects the approach taken by researchers to find behavior-influencing compounds by examining volatile compounds from flowers or fruit (1, 6, 36, 37, 52, 79, 98, 119) or the occasional serendipitous discovery (47, 96), and by examining structural or aroma analogies of these compounds (47, 124). Thrips lures can be grouped in a number of ways (56, 58) and include a broad range of different classes of chemical compounds, but the identified compounds are mainly derivatives of either benzene or pyridine (Supplemental Table 2). As noted, many of these have been identified from flowers or fruits and those that have not may be below the level of detection for current technology or just happen to trigger the same thrips olfactory receptor neurons (124). The vast majority of thrips species for which lures have been identified, inhabit flowers or feed on fruit and many are plant pests, but some are pollinators (109, 119). In general, non-flower inhabiting thrips do not respond (52, 131). Methyl isonicotinate (MI) is probably the most extensively studied thrips non-pheromone semiochemical, demonstrating a behavioral response that results in increased trap capture of at least 12 thrips species, including cosmopolitan virus vectors such as WFT and OT (127). MI is one of several patented 4-pyridyl carbonyl compounds, and is the active ingredient of the commercial lures, such as Lurem-TR (57). MI fulfils all the characteristics necessary for an effective thrips lure: (1) low toxicity –relatively safe for human use, (2) volatile –vaporises under ambient trapping conditions, (3) stable – can be stored a long time (e.g. more than a year), (4) low cost – relatively inexpensive for established pest monitoring programs, and (5) efficacious – increases trap capture of males and females of key thrips pest species (122).

Factors affecting responses. Increasing dose can increase or decrease responses, depending on the compound, in olfactometer studies (walking response) (22, 59, 79), but there is increasing evidence for a dose response in trapping studies (flying response): an increase in dose generally equates with increased trap catches (36, 37, 123). Studies on the role of plant volatiles in thrips pollination of cycads indicated a dose-dependent response of *Cycadothrips chadwicki* toβ-myrcene, which acted in high concentrations as a repellent and in low concentrations as an attractant (119).

The lack of an additive or synergistic effect from compound mixtures (36, 37, 79, 129, 140) suggests a relatively simple sensory system with single receptors for generic compounds or poor sensory integration between receptors. Only Binyameen et al. (10) have observed a small but significant additive trapping effect, for the response of OT to eugenol and ethyl isonicotinate combined.

Strong odors given off by host plants may compete with or mask the effect of a lure. Davidson et al. (19) found that traps with ethyl isonicotinate caught significantly more OT in a grass field than similar traps in an onion crop, suggesting that onion crop characteristics, such as odor, might have influenced trap capture. Conversely, Teulon et al. (125) have shown season-long efficacy for MI when trapping WFT in a nectarine orchard, despite the presumed presence of competing and changing host-plant odors over time. Additionally, Koschier et al. (60) have shown that MI remains attractive for WFT in the presence of competing odors in an olfactometer.

Odor from lures may increase thrips capture in traps without lures if they are near each other (121, 123, 130), indicating that previous work might have underestimated the effect of compounds increasing trap capture (48), especially where there was a high concentration of baited traps in a given area.

Well-fed female WFT are less responsive to visual and/or olfactory cues in a Y-tube olfactometer or wind tunnel than starved thrips (18). This implies that resident thrips found within a crop may be less responsive to lures than a non-resident searching for new hosts.

## Repellents and Deterrents

Prior to alighting on a potential host plant, thrips use plant volatiles as olfactory cues to avoid unsuitable hosts at a distance and avoid unsuitable plant parts at close range. Repellents cause insects to move away from an odor source (28) and are identified in bioassays that prevent contact between the insect and the stimulus (27), such as olfactometers in the laboratory or traps in the field.

Plant odors emitted by hosts with low suitability for oviposition, such as garlic (*Allium sativum*) and celery (*Apium graveolens*), repelled WFT females in olfactometer experiments (14). *Limothrips cerealium* and *Haplothrips aculeatus* were attracted by odors of oat (*Avena sativa*) spikelets, the plant parts they inhabit, but avoided the odors of oat leaf sheaths and stems (44). Colonisation of onion plants with the endophytic fungus *Hypocrea lixii* may result in the production of volatiles that cause OT to prefer endophyte-free onion plants over colonised onions in the olfactometer. Moreover, on colonised plants, feeding and oviposition were reduced (87). Jones et al. (49) found that *F. schultzei* responded negatively to flower and leaf odors of its primary host *Malvaviscus arboreus*, and suggested that this species uses visual cues for host location. Since *M. arboreus* is hummingbird-pollinated, it may have developed defensive flower volatiles to repel pollen-consuming insects such as thrips. *Frankliniella schultzei* inhabits flowers and might use the volatiles to avoid *M. arboreus* leaves. Cyanogenic glycosides in *Sambucus nigra* influence the behavior of the pollinating thrips species *T. major*. Although the level of prunasin and sambunigrin is low in floral tissues, increased amounts of these substances before and after flowering deter the thrips from unopened flower buds and developing fruits (109).

Defensive phytochemicals hold some promise for plant breeders in search of resistant cultivars. However, evidence for host-plant resistance to thrips deriving from repellent volatiles is scarce. McKellar et al. (80) found that volatile chemicals released from leaf tissues may be involved in resistance of chrysanthemum to WFT. *Megalurothrips sjostedti* females clearly avoided odors emitted by several cowpea cultivars during their vegetative stage and floral volatiles of one specific cultivar. Volatile analyses and further olfactometer experiments showed that (*E*)-2-hexenal repelled the thrips (29).

It is noteworthy that the repellence of some plant odors can be attributed to single constituents. This may apply to plant extracts and essential oils as well. *Megalurothrips sjostedti* proved to be repelled by volatiles from freshly cut lemongrass (*Cymbopogon citratus*) leaves and also by one of the major compounds in these volatiles, the monoterpenoid citral (30).

Abtew et al. (2) screened numerous plant extracts for olfactory responses of *M. sjostedti* females and found that *Piper nigrum*, *Cinnamomum verum* and *Cinnamomum cassia* extracts were the strongest repellents. However, single constituents of these extracts have not yet been tested with thrips. Linalool as a pure compound in olfactometer experiments (61) and as a constituent of *Origanum majorana* essential oil in field trapping trials elicited negative responses from OT. Otherwise, eugenol as part of *Ocimum gratissimum* essential oil repelled OT in the field (136), but not in the olfactometer (61). The essential oil of rosemary (*Rosmarinus officinalis*) also repels OT at a relatively high concentration of 10 % (62).

Olfactory repellence in thrips has been repeatedly demonstrated to be concentration dependent, with some volatiles being effective solely at specific concentrations, and others at a range of concentrations (59).

While repellents may prevent landings of adult insects on a plant, deterrents present on the plant surface or in the plant act after alighting and may inhibit feeding or oviposition. Discrimination between repellents and deterrents is sometimes difficult because volatilization of compounds may give continued olfactory input after contact with the plant (101). The interaction of olfactory and gustatory cues in host finding and acceptance of thrips was demonstrated in choice assays when WFT were attracted to linalool-emitting chrysanthemums, but this initial preference reverted to deterrence, probably caused by non-volatile linalool glycosides in the plant (141).

Increasing numbers of studies investigate non-volatile compounds from chemical classes that are involved in thrips resistance in plants. Hybrids of *Jacobaea vulgaris* and *J. aquatica*, which are resistant to WFT, showed a higher content of the two pyrrolizidine alkaloids jaconine and jacobine *N*-oxide (16, 68) and the flavonoid kaempferol glucoside than susceptible hybrids (68). In chrysanthemum, two phenylpropanoid compounds conferred resistance against WFT; resistant cultivars contained higher amounts of chlorogenic acid and feruloyl quinic acid (70). Carrot (*Daucus carota*) cultivars containing higher amounts of the flavonoid luteolin, the phenylpropanoid sinapic acid and the amino acid β-alanine sustained less feeding damage by WFT (69). Acylsugars exuded from type IV trichomes on flowers of *Solanum lycopersicum* and interspecific hybrids (8), as well as a purified extract from *Lycopersicon pennellii* (67), deterred WFT from oviposition. In addition to those defensive metabolites that are constitutively present in the plant, others are produced in response to thrips infestation (112). For example, Schütz et al. (108) showed that WFT feeding on Papaveraceae plants induced the production of benzophenanthridine alkaloids in the leaves, and in choice assays the thrips avoided contact with these metabolites. WFT feeding on tomato plants resulted in the induction of jasmonic acid-associated defenses with changes in leaf trichome-associated volatiles. These volatiles may be responsible for repelling conspecifics from contacting the plants (38).

Essential oils and pure compounds have been applied to crop plants to test their effects on the behaviors of thrips, with the aim of using defense-related secondary metabolites for crop protection. Laboratory studies have identified, for instance, that lavender (*Lavandula angustifolia*) or marjoram (*O. majorana*) essential oils deter OT from feeding and oviposition when sprayed on leek (*Allium ampeloprasum*) (62, 63). OT females avoided direct contact with the phenylpropanoid eugenol, and their feeding and egg-laying activity on treated leek was clearly reduced (61, 63). Effects were typically detected at application rates in the range of 0.01-0.1 µl oil cm-2. Application of eugenol not only inﬂuenced feeding and oviposition, but also the activity patterns of the thrips. Behavioral observations revealed that the periods when OT females fed and laid eggs were shortened and the periods when they were inactive or moving across treated leek surfaces were prolonged (102). Secondary metabolites may modify behaviors of immature thrips as well. The application of *cis*-jasmone and methyl jasmonate, two jasmonic-acid derivatives, deterred WFT second-instar larvae from feeding and caused them to leave jasmonate-treated bean plants by migrating to the soil (32). Adult WFT feeding and oviposition was significantly reduced on bean leaves treated with *cis*-jasmone or methyl jasmonate, particularly when mixed at a ratio of 1:1 with a compound from a different chemical class. The deterrence proved to be concentration dependent and was not altered by repeated short-term or continuous long-term exposures of WFT females. The 1:1 mixtures reduced the probability that thrips habituated to the deterrent compounds when applied at concentrations required to produce 50% feeding deterrence (33, 34).

# PEST MANAGEMENT

Research and application of semiochemicals for thrips pest management is still at a rudimentary stage with the current utilisation mainly for thrips monitoring. There are significant opportunities to extend the use of semiochemicals beyond their current use into several new directions for thrips management in indoor and outdoor crops (25, 53, 126, 127).

## Monitoring

Current lures improve the effectiveness of colored traps by increasing thrips capture, leading to earlier and more accurate detection and improving presence/absence estimates at low densities (20, 41, 107, 131). Muvea et al. (88) found a high correlation between the number of thrips on MI-baited blue sticky traps and the absolute estimate of thrips density on plants.

Commercial pheromone-based monitoring products are typically small rubber septa impregnated with about 30 µg of pheromone that can be attached to a trap (e.g. ‘Thripline’ from Bioline AgroSciences and ‘ThriPher’ from Biobest). One characteristic of lures based on pheromones is that they are species-specific, which can be useful for detection of a single species when others are present. Commercial monitoring products based on plant-derived semiochemicals typically consist of a controlled release sachet with about 3 ml of semiochemical that can be hooked onto a trap (e.g. ‘Lurem-TR’ from Koppert Biological Systems and ‘P178 attractant’ from ChemTica) (92). These can attract several species of thrips, which is an advantage when multiple pest species are present in crops.

## Mass Trapping

Mass trapping can be an effective method to reduce insect damage to crops. Mass trapping of WFT with blue sticky traps combined with the grower’s IPM program was cost-effective in a commercial strawberry crop in the UK (107). In this experiment, addition of WFT pheromone doubled trap catches, but the increase in control efficacy compared to coloured sticky traps alone was not significant. There are, however, numerous (many anecdotal) reports of the use of lures with colored sticky traps to successfully mass-trap thrips. For example, reports that Lurem-TR with colouredsticky traps has been used to mass-trap thripssuccessfully in greenhouses with crops such asrose (Victoria, Australia), capsicum (Tunisia) and sweet pepper (Morocco) (127) and that pheromone traps can manage WFT in table grapes in Spain (75). However, scientific evidence is not available to support these conclusions (53, 127), and other published reports of successful mass trapping with MI appear to be poorly designed (127). Incorporation of a semiochemical into roller traps, including by microencapsulation (e.g. ‘Optiroll Super plus’ from Russell IPM Ltd, UK, which incorporates WFT pheromone) might prove to be beneficial for mass trapping. Mass trapping integrates well with other control measures and mass trapping with WFT pheromone in strawberry in the UK did not increase the catch of beneficial predators (106).C:\GetARef\Refs\Kirk.ref #393;

## Mating Disruption

The use of aggregation pheromone or antiaphrodisiac pheromone for mating disruption is yet to be tested. Since most thrips species have arrhenotokous reproduction, the prevention of mating will increase the proportion of males in each generation, so it would take two generations to reduce the population size, but this does not take long in thrips (53).

## Increasing Efficacy of Natural Enemies

The response of beneficial organisms to thrips semiochemicals has been recorded in several studies, with a number of compounds proving to influence their behavior (Supplemental Table 4). For example, species of the predatory bug *Orius* are attracted or arrested by aggregation pheromone (117, 134, 138), alarm pheromone (117) and MI (21), indicating possibilities for manipulating populations of thrips and *Orius* within a crop to maximise predation. Variable responses for different predators and parasites would need to be considered for practical use, but there is an opportunity to manipulate thrips populations by strategic use of these thrips semiochemicals to maximise the impact of natural enemies and to monitor their density.

## Lure and Infect

Screen-house trials have shown increased uptake of entomopathogenic fungi and mortality of WFT in the presence of an auto-inoculative device with Lurem-TR in French beans (90). However, the MI volatiles bring about reduced conidial viability of the entomopathogens *Metarhizium anisopliae* and *M. brunneum* (82, 90), unless there is a degree of separation between the lure and the fungus (82). The use of WFT aggregation pheromone for lure and infect is yet to be tested (53).

## Stand-Alone Applications of Repellents and Deterrents

Compounds that cause thrips to spend less time in a treated area might reduce the incidence of economic damage. Allsopp et al. (5) demonstrated that the antifeedant compounds carvacrol, thymol and methyl salicylate deterred WFT oviposition, even when applied to fragrant plum blossoms. Reitz et al. (100) applied essential oils combined with kaolin to tomatoes in the field, thus reducing the incidence of thrips-vectored *Tomato spotted wilt tospovirus* infections of the plants. Because the volatility of essential oils is a major limiting factor for practical use, Picard et al. (97) incorporated the oils into alginate and methyl cellulose polymers. WFT females avoided bean leaves treated with winter savory (*Satureja montana*) essential oil formulated with the alginate, and this effect was maintained over several days. Pyrethrins extracted from *Tanacetum cinerariifolium* (142) and azadirachtin, a compound in neem (*Azadirachta indica*) seed oil (95), are botanical insecticides widely used against many agricultural insect pests, and also show deterrent properties against WFT.

## Push-Pull

Proof-of-concept experiments using MI and a thrips repellent, the essential oil of marjoram (*O. majorana*), have shown that the number of OT on white sticky traps can be manipulated to cause a push-pull effect (136). The concept of push-pull using MI and thrips repellents has been further demonstrated in Y-tube olfactometer experiments with WFT, including those in circumstances with competing background plant odors (60). Nonetheless, experiments that better reflect actual cropping systems are required to identify the likely success of this method for thrips pest management.

## Trap Plants and Spot Treatment

We have observed thrips congregating on crop plants near lures containing MI. Thrips congregating at these points could be managed by killing them with either pesticides or biological control agents as required, rather than by treating the whole crop. There is evidence for the efficacy and positive cost:benefit of spot sprays of *M. anisopliae* for managing *M. sjostedti* infesting cowpea in Kenya (81)*.* As noted above, some natural enemies respond to MI and pheromones, indicating that pests (and at least some natural enemies) could be aggregated within a crop to maximise predation.

## Activator for Insecticides and Biologicals

Thrips are thigmotactic and seek out confined spaces where they are hard to reach by pesticides or biological control agents, including predators and spores of entomopathogenic fungi. More active and exposed thrips could be more susceptible to insecticides and probably also at greater risk from natural enemies. The WFT aggregation pheromone brought thrips out of hiding places on plants (93) and MI blown over WFT on leaf discs in the laboratory increased their walking and take-off behaviour (135), both potentially providing an opportunity to increase exposure of thrips to a range of control tactics. There is some evidence that the addition of the WFT alarm pheromone increased the effectiveness of insecticides in field trials (17), and an industry journal reported on the use of WFT aggregation pheromone to increase the efficacy of insecticides for WFT control by introducing it to a greenhouse shortly before treatment (42).

## Integration

Given that a range of semiochemical approaches may be useful for any given thrips species, it is likely that integration of a number of approaches, including the use of semiochemicals, would achieve the greatest impact on management (13, 131).

# FUTURE ISSUES

1. The behavioral responses of thrips to semiochemicals need to be studied. We should move on from just identifying semiochemicals that increase trap catch. This, in turn, can improve the effectiveness of semiochemicals in pest management by allowing us to predict outcomes under a wide range of spatial configurations.

2. The focus of research should shift from olfactory stimuli in isolation to the interactions with other stimuli, particularly vision, which may occur simultaneously or in rapid succession.

3. Extrinsic and intrinsic factors that explain variable responses to semiochemicals should be considered.

4. The impact of semiochemicals on non-target organisms, including beneficials, needs to be investigated.

5. The use of semiochemicals in integrated pest management of thrips needs to move beyond monitoring and be developed for control.

6. Dispensers and formulation need to be developed for particular uses in pest management.

7. Thrips should be used as a model system for semiochemical responses of small insects that have limited ability to fly upwind. This can contrast with the majority of work on semiochemical responses of large insects, such as moths and beetles.

# DISCLOSURE STATEMENT

WDJK is a named inventor on a patent for the use of aggregation pheromone to control thrips (WO/2003/055309) and his employer (Keele University) receives royalty income. DAJT is a named inventor on a patent for the use of pyridine derivatives to control thrips (WO/2005/046330) and his employer (the New Zealand Institute for Plant and Food Research Ltd) receives royalty income. Apart from this, the authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Table 1 The male-produced aggregation pheromones identified so far in thrips, which are all from the family Thripidae

|  |  |  |  |
| --- | --- | --- | --- |
| Thrips species | Major compound | Minor compound | References |
| *Frankliniella intonsa*  | Neryl (*S*)-2-methylbutanoate | (*R*)-Lavandulyl acetate | (143) |
| *Frankliniella occidentalis*  | Neryl (*S*)-2-methylbutanoate | (*R*)-Lavandulyl acetate | (43) |
| *Megalurothrips sjostedti*  | (*R*)-Lavandulyl 3-methylbutanoate | (*R*)-Lavandulol | (91) |
| *Megalurothrips usitatus*  | (*E*,*E*)-Farnesyl acetate | not found | (73) |
| *Thrips palmi*  | (*R*)-Lavandulyl 3-methyl-3-butenoate | not found | (3) |

# SUPPLEMENTAL MATERIAL

Supplemental Table 1 List of thrips species and the semiochemical compounds they produce

Supplemental Table 2 List of thrips species and the non-pheromone semiochemicals produced by plants reported from published literature to attract thrips in laboratory assays or to increase capture of thrips on traps in the field

Supplemental Table 3 List of thrips species and the non-pheromone semiochemicals produced by plants that act as repellents and/or deterrents

Supplemental Table 4 List of beneficial arthropods and the effects of thrips semiochemicals reported from published literature

# TERMS AND DEFINITIONS

Aggregation pheromone: a pheromone produced by one sex that attracts both sexes.

Alarm pheromone: a pheromone that alerts others to a threat

Allomone: a semiochemical that benefits the emitter in one species and harms the receiver in a different species

Antiaphrodisiac pheromone: a pheromone that deters mating, usually applied by males to females to deter other males from mating with that female

Arrestant: a chemical that slows linear progress of a responder by decreasing its speed or increasing its rate of turning

Attractant: a chemical causing a responder to make movements oriented toward the stimulus source

Deterrent: a chemical that inhibits feeding or oviposition

Kairomone: a semiochemical that harms the emitter in one species and benefits the receiver in a different species

Phlaeothripidae: the largest family of thrips, also known as Tubulifera, recognisable by a distinctive tube at the end of the abdomen

Repellent: a chemical causing a responder to make movements oriented away from the stimulus source

Sex pheromone: a pheromone produced by one sex that lures the other sex for mating or indicates readiness to mate

Synomone: a semiochemical that benefits the emitter in one species and the receiver in a different species

Thripidae: the second-largest family of thrips, which contains most of the pest species

Trail pheromone: a pheromone that marks a trail on a substrate and allows others of the same species to follow that trail