REVIEW ARTICLE

The aggregation pheromones of thrips (Thysanoptera) and their potential for pest management

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Abstract. Aggregation pheromones have been identified and tested in the field for *Frankliniella occidentalis* and *Thrips palmi*. These pheromones are produced by adult males and attract both males and females. They are likely to be widespread across the Thripidae and identification is in progress for several other pest species. Aggregation pheromones are used commercially for monitoring and activation. Field trials have shown they can be cost effective for mass trapping when used as part of an integrated pest management (IPM) programme. Use for other approaches, such as lure and kill and mating disruption have not yet been tested. A better understanding of the role of these pheromones in the mating behaviour of thrips is needed and this may suggest further ways of developing their potential for pest management.

Key words: *Frankliniella occidentalis*, *Thrips palmi*, *Frankliniella intonsa*, pheromone, neryl (*S*)-2-methylbutanoate, (*R*)-lavandulyl acetate, (*R*)-lavandulyl 3-methyl-3-butenoate, monitoring, mass trapping, IPM

Introduction

Thrips are major pests of agricultural and horticultural crops, causing damage by feeding and the transmission of plant pathogens, particularly tospoviruses (Childers, 1997; Ullman *et al.*, 1997; Whitfield *et al.*, 2005). They occur throughout the world, in both tropical and temperate regions, and several species are invasive (Kirk and Terry, 2003; Cannon *et al.*, 2007). Thrips are particularly difficult to control with pesticides, because they hide in small spaces on plants and rapidly develop resistance to insecticides (Gao *et al.*, 2012). Hence, new approaches to thrips management are needed.

Pheromones have been widely used for management of other insect pests and there are many

ways in which they can be used (Howse *et al.*, 1998). Several types of pheromone have been identified in thrips. A larval alarm pheromone has been identified in the western flower thrips, *Frankliniella occidentalis* (Pergande), and has shown potential to enhance the effects of insecticides (Teerling *et al.*, 1993; MacDonald *et al.*, 2002; Cook *et al.*, 2002). An adult-male-produced contact pheromone has been identified, also in *F. occidentalis*, but since it appears to act only by contact, its potential for pest management appears to be limited (Olaniran *et al.*, 2013). Anti-aphrodisiac pheromones have been discovered in *Echinothrips americanus* Morgan (Krueger *et al.*, 2016) and such pheromones could be useful for mating disruption (see below). Aggregation pheromones have now been identified from several species and have the potential to be used for trapping and behaviour modification in

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a range of possible applications. The aim of this paper is to review current knowledge of aggregation pheromones in thrips and discuss their potential for pest management.

Field observations of aggregation

Some common thrips species can form large aggregations. For example, *Thrips atratus* Haliday, *Thrips flavus* Schrank, *Thrips fuscipennis* Haliday, *Thrips major* Uzel, *Thrips vulgatissimus* Haliday and *Frankliniella intonsa* (Trybom) form aggregations on flowers (Morison, 1957; Kirk, 1985, 1996) (Fig. 1), *F. occidentalis* males form aggregations on white surfaces (Terry and Gardner, 1990), *Frankliniella schultzei* (Trybom) males form aggregations on the upper surfaces of flowers (Milne *et al.*, 2002), *Pezothrips kellyanus* (Bagnall) males form aggregations on leaves and fruit (Webster *et al.*, 2006), males of *Parabaliothrips newmani* Gillespie, Mound & Wang form aggregations on leaf buds (Gillespie *et al.*, 2002) and *Megalurothrips sjostedti* (Trybom) males form aggregations on leaves (Niassy *et al.*, 2016) (Fig. 2). Within such aggregations, fighting between males has been observed in *F. occidentalis* and *F. intonsa* (Terry and Gardner, 1990; Kirk, 1996). The formation of aggregations strongly suggests that pheromones are involved. These could be sex pheromones, where one sex attracts the opposite sex, or aggregation pheromones, where one sex attracts both sexes.

However, aggregations have not been observed in some common species, such as *E. americanus* (Krueger *et al.*, 2015) or *Thrips palmi* Karny, and it is not clear whether this reflects a real behavioural difference or just that these species have not been observed in the right place at the right time. In *F. occidentalis* and *M. sjostedti*, the extent of aggregation appears to vary considerably with the season, time of day and weather conditions (Terry and Gardner, 1990; Terry and Dyreson, 1996; Niassy *et al.*, 2016), so aggregations are not obvious and can be easily overlooked.

Pore plates and sternal glands

The adult males of many species of thrips have pore plates (*areae porosae*) on the abdominal sternites, which are visible in specimens on microscope slides. Mound (2009) presented photographs of many of these and estimated that more than 60% of genera in the family Thripidae have pore plates in the males, so they are widespread. The pores suggest that pheromones are released from these areas, and examination of the underlying tissues has found glandular tissue consistent with pheromone production (Bode, 1978; Moritz, 1997; Sudo and Tsutsumi, 2002; Shitatani and Tsutsumi, 2005, 2006; El-Ghariani and Kirk, 2008; Krueger *et al.*, 2015). The

evidence so far suggests that sternal glands produce pheromones, which are released through the pore plates. Although it is likely that the sternal glands produce aggregation pheromone, this has not yet been proved. When the first aggregation pheromone was identified in *F. occidentalis* (Hamilton *et al.*, 2005), it was the only known male-produced pheromone and the sternal glands were present only in males, so there was strong circumstantial evidence that these glands produced the aggregation pheromone. In addition, a pheromone that is released into the air to act at a distance would need to be produced in relatively large quantities and require a large amount of glandular tissue to produce it, so the large sternal glands, which are repeated down the abdomen, were obvious candidates. However, the recent discovery of a second adult-male-produced pheromone in *F. occidentalis* complicates the issue (Olaniran *et al.*, 2013), particularly as the production rates of the two pheromones are comparable (Dublon *et al.*, 2008; Olaniran *et al.*, 2013). Do the sternal glands produce both aggregation pheromone and contact pheromone or are either or even both of them produced elsewhere? If sternal glands do produce aggregation pheromone, then aggregation pheromones are likely to be widespread, at least in the Thripidae.

There is circumstantial evidence that the sternal glands produce aggregation pheromone from the association between the two. The finding that male *M. sjostedti* aggregate on leaves suggested the presence of an aggregation pheromone (Niassy *et al.*, 2016), but the species was thought to have no pore plates (Mound, 2009). Subsequent investigation showed that small pore areas and sternal glands were indeed present (Krueger *et al.*, 2015). So far, all the thrips species where there is evidence for the production of aggregation pheromone have sternal glands.

Bioassays

Some of the first direct evidence of a male-produced pheromone came from Y-tube olfactometer bioassays with *F. occidentalis*. In experiments in England, adult males and females responded by walking towards the odour of live males (Hamilton and Kirk, 2003; Kirk and Hamilton, 2004), whereas in the Netherlands, adult females responded but not males (de Kogel and van Deventer, 2003). More recently, experiments in China showed that adult males and females responded to the odour of live males (Zhu *et al.*, 2012). The reason for the discrepancy in male response in a Y-tube remains unexplained, although both males and females respond in flight to synthetic aggregation pheromone (see below).

Fig. 1. Aggregation of adult males of *Thrips fuscipennis* and *Thrips major* on a white flower of *Calystegia sepium* (L.) R.Br. in the UK. Photo (black and white): W. D. J. Kirk.

Fig. 2. Aggregation of adult males of bean flower thrips, *Megalurothrips sjostedti*, on a leaf of cowpea, *Vigna unguiculata* (L.) Walp. in Kenya. Photo: S. Niassy.

This initial uncertainty about whether the pheromone attracted the opposite sex only or both sexes led to it being referred to initially in publications as a sex pheromone and then later as an aggregation pheromone. Although the term 'aggregation pheromone' is widely used for a pheromone that is produced by one sex and attracts both sexes, the term can be misleading because such responses do not necessarily produce observable aggregations.

It is to be expected that an adult-male-produced pheromone would attract females for mating, but in species where mating involves male aggregations, the same pheromone can be used by males to locate the aggregation, so both sexes will then respond to the pheromone in an olfactometer or on traps. The finding that male *T. palmi* are attracted to the male-produced aggregation pheromone suggests that the males aggregate (Akella *et al.*, 2014), even though direct evidence for such a behaviour does not exist.

Differences in response between the sexes have been recorded not just within a species but also between species. In Australia, live males of *F. schultzei* increased trap catches of adult females but not adult males (Milne *et al.*, 2002, 2007), whereas in a Y-tube olfactometer, both males and females responded to the odour of live males of *T. palmi* (Akella *et al.*, 2014). Filter paper exposed to adult male *P. kellyanus* was responded to by both males and females (Webster *et al.*, 2006). This variation in response between the sexes could be the result of different pheromones being used in different circumstances or differences in responsiveness between the sexes at different times of day. The responses can only be fully understood by identifying the pheromones involved and comparing the responses to synthetic and natural pheromones.

Zhu *et al.* (2012) gave adult thrips a choice in a Y-tube olfactometer between the odour of live males of *F. intonsa* and the odour of live males of *F. occidentalis*. The males and females of each species significantly preferred the arm with conspecific males. Since the same two adult-male-produced headspace volatiles have been identified from both species (Table 1), it was concluded that the males and females must be detecting their own species by the ratio of the two compounds. However, this has not been demonstrated by using synthetic pheromones and it is possible that other compounds are involved.

The addition of synthetic aggregation pheromone to traps increased trap catches of males and females in commercial crops for *F. occidentalis* and *T. palmi* (Hamilton *et al.*, 2005; Akella *et al.*, 2014). The landing response appears to be dependent on the presence of a visual stimulus, because the pheromone attracts very few thrips when used with black or clear traps (Sampson *et al.*, 2012). This suggests that there is an interaction between the olfactory response and the visual response, which may explain why natural aggregations are usually on brightly coloured objects (see above). Host plant volatiles could play a role, but this has not been tested. Since trapping experiments have nearly always been carried out in crops, plant odour was already present.

Pheromone identification

Aggregation pheromones act at a distance and so must be volatile compounds that can be detected in headspace volatiles. They can therefore be collected by solid-phase microextraction (SPME) (Hamilton *et al.*, 2005) or by entrainment on a column, such as Tenax (Akella *et al.*, 2014). The compounds can then be identified by coupled gas chromatography-mass spectrometry (GC-MS). The amounts of compound that are collected are very small, which rules out identification by nuclear magnetic resonance (NMR). Instead, the retention times and mass spectra have to be matched to a library of similar compounds. The main compounds identified so far are monoterpenoid esters of 5-carbon acids. Unfortunately, such compounds are extremely numerous because there are many monoterpene alcohols and many different five-carbon acids, and their mass spectra are very similar. Identification can take a long time, particularly if candidate compounds have to be specially synthesized to check the match. The compounds identified so far have all been chiral, which adds further stages of separating the enantiomers on a chiral column by GC, synthesizing the enantiomers and then matching them.
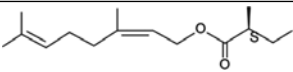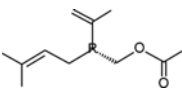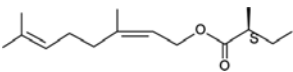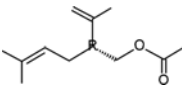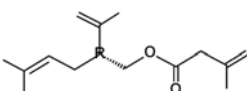
The approach to finding compounds that are likely to be pheromones has been to compare adult-male-produced headspace volatiles with adult-female-produced volatiles and look for large peaks by gas chromatography. So far, this has revealed male-specific compounds but no female-specific compounds. Compounds identified in this way are likely to be pheromonal, but their biological role as a pheromone or a pheromone component needs to be demonstrated by showing the effect of synthetic compounds. This is also a safeguard against errors in identification. The headspace volatiles identified from *F. occidentalis* and *T. palmi* have been tested in the field (Hamilton *et al.*, 2005; Akella *et al.*, 2014), but this has not been done so far for *F. intonsa* (Zhang *et al.*, 2011).

Roles of major and minor compounds

Two compounds were identified in the headspace volatiles entrained from adult male *F. occidentalis* that were not produced by adult females.

Table 1. Adult-male-produced headspace volatiles of thrips identified so far. Analysis is in progress for several other thrips species.

Species	Compound name	Structure	Reference
Frankliniella occidentalis	[+]neryl (*S*)-2-methylbutanoate		Hamilton *et al.*, 2005
	(*R*)-lavandulyl acetate		Hamilton *et al.*, 2005
Frankliniella intonsa	neryl (*S*)-2-methylbutanoate		Zhang *et al.*, 2011
	(*R*)-lavandulyl acetate		Zhang *et al.*, 2011
Thrips palmi	[+](*R*)-lavandulyl 3-methyl-3-butenoate		Akella *et al.*, 2014

[+] = compounds that have been tested in the field and demonstrated to act as an aggregation pheromone.

The major compound, neryl (*S*)-2-methylbutanoate was shown to increase trap catches of adult males and females, but the minor compound, (*R*)-lavandulyl acetate did not increase trap catches, while a 1:1 blend of the two compounds caught no more than the major compound alone (Hamilton *et al.*, 2005). Further experiments with a range of doses and ratios showed no increase or a decreased trap catch with the addition of the minor compound (unpublished data; Dublon, 2009). This leaves the role of the minor compound uncertain. The biochemical synthesis pathways of the two compounds are clearly different, so one is not a precursor or a by-product of the other.

A consistent ratio of the two compounds would suggest that they are components of one pheromone. Measurements of the ratio of the two compounds with SPME in England found the minor: major ratio varying between 1: 0.8 and 1: 5 (Hamilton *et al.*, 2005). In contrast, measurements with SPME in China showed a mean ratio of 1:12.9 for *F. occidentalis*, which was markedly different from the mean ratio of 1:1.7 for *F. intonsa* (Zhu *et al.*, 2012). The evidence so far is unclear.

Laboratory bioassays with the minor compound, (*R*)-lavandulyl acetate, have shown that it affects the behaviour of adult male and female *F. occidentalis*, but differently, and the observed effects led to the suggestion that it may be a mating pheromone (Olaniran, 2012).

A minor compound was not found in the headspace volatiles of male *T. palmi*, so it will be interesting to see if minor compounds are found in the headspace volatiles of males of other species and whether they can shed further light on their role.

All the male-produced headspace volatiles identified so far have been chiral (Table 1), and the evidence so far is that the response to the aggregation pheromone is enantiomer-specific. Traps baited with racemic neryl 2-methylbutanoate (equal amounts of neryl (*S*)-2-methylbutanoate and neryl (*R*)-2-methylbutanoate) caught significantly fewer *F. occidentalis* than unbaited control traps or traps with the male-produced enantiomer (neryl (*S*)-2-methylbutanoate) (Dublon, 2009).

Potential for IPM

Monitoring

The respective aggregation pheromones increase sticky trap catches of *F. occidentalis* (Hamilton *et al.*, 2005; Gómez *et al.*, 2006; Broughton and Harrison, 2012; Sampson *et al.*, 2012; Sampson and Kirk, 2013; Sampson, 2014; Broughton *et al.*, 2015) and *T. palmi* (Akella *et al.*, 2014). The ratio of trap catch between pheromone traps and controls is higher for less visually attractive traps, but for the most visually attractive commercial sticky traps, which are already highly attractive, the ratio is typically between about 1.5:1 and 4:1 (Sampson *et al.*, 2012; Broughton *et al.*, 2015). The amount of pheromone needed to have this effect is extremely small, about 30 μg, and can be impregnated in a rubber septum or in the trap itself.

Species specificity of the aggregation pheromones has not been tested very much, but the evidence so far is that other species are not attracted, as would be expected. For example, the aggregation pheromone of *F. occidentalis* increased trap catches

of *F. occidentalis*, but not of *Thrips imaginis* Bagnall or *Thrips tabaci* Lindeman, in fruit orchards in Western Australia (Broughton and Harrison, 2012).The aggregation pheromone showed no significant effect on catches of *T. tabaci* or *Thrips angusticeps* Uzel in sweet pepper crops in Spain (Dublon, 2009).

Since aggregation pheromones are species specific, they are suitable for use in crops dominated by a single thrips species. They also have the advantage of species specificity for monitoring or detection of particular species that are quarantine pests. This specificity also means they are unlikely to attract beneficial insects (Sampson *et al.*, 2012). In comparison, non-pheromone semiochemical attractants (Teulon *et al.*, 2017), which are based on plant attractants, tend to be attractive to several thrips species as well as to beneficial insects and require higher release rates and thus larger volumes on traps.

The aggregation pheromone of *F. occidentalis* is sold commercially, under licence, by Bioline Agrosciences Ltd (formerly Syngenta Bioline Ltd) as Thripline™ ams and by Biobest Belgium N.V. as ThriPher. The pheromone is impregnated into rubber lures and sold in sachets of 10 lures. Growers can attach the lures to sticky traps to increase trap catch.

Activation

It could be predicted that an aggregation pheromone would cause adult thrips to become more active and seek out aggregations for mating, since that is its function. Bioassays have shown that adult female *F. occidentalis* increase the amount of time spent walking and take off more often in the presence of the aggregation pheromone, even at doses as low as 50 pg (Olaniran, 2012).

Some commercial recommendations make use of this behaviour, although the experimental evidence has not been fully published. One company recommends that aggregation pheromone lures are placed in the CO_2 dosing system of a greenhouse prior to a pesticide treatment to activate the thrips and increase the effect of the insecticide. It is reported that when the pheromone is installed 30 minutes before treatment with insecticides there is a 30% greater reduction in thrips numbers (GreatRex, 2009). The same approach could well increase the effectiveness of biopesticides or biological control agents.

An increase in activity could potentially increase the spread of a plant virus if it increased the frequency of long flights between plants. However, this has not been tested. It is also possible that the pheromone arrests or induces landing in flying thrips, in which case it could reduce the spread of a plant virus.

Mass trapping

Mass trapping with aggregation pheromone on sticky roller traps can be an effective way of reducing thrips populations when used as part of an integrated pest management (IPM) programme. It is compatible with biological control so long as the trap colour and pheromone are not attractive to the biological control agents. The approach has been tested in semi-protected strawberry crops in the UK (Sampson and Kirk, 2013). Mass trapping of *F. occidentalis* using blue sticky roller traps reduced adult thrips numbers per flower by 61% and fruit damage by 55%. The addition to the traps of the *F. occidentalis* aggregation pheromone, neryl (*S*)-2-methylbutanoate, doubled the trap catch and reduced adult thrips numbers per flower by 73% and fruit damage by 68%. Cost−benefit analysis showed that mass trapping of thrips using blue sticky roller traps with pheromone can be cost effective in high-value crops (Sampson and Kirk, 2013). Mass trapping with aggregation pheromone on blue sticky traps has been used successfully to manage *F. occidentalis* in table grapes in Spain (Lucas-Espadas, 2013). Trials with aggregation pheromone on blue sticky traps in Romania concluded that mass trapping could be useful for management of *F. occidentalis* in glasshouse cucumber crops (Covaci *et al.*, 2012).

Lure and infect

The use of a semiochemical in an auto-dissemination device has been used to control *F. occidentalis* (Niassy *et al.*, 2012) but the approach has not yet been tried with aggregation pheromone. In this regard, it will be essential to assess the compatibility between the thrips aggregation pheromone and the entomopathogenic fungi.

Push−pull

An aggregation pheromone could be used as part of a push−pull system to pull thrips towards banker plants or trap crops. It could also be used to pull thrips to hot-spots that could be spot-treated with insecticide, reducing the use of insecticide and the cost of labour. However, none of these approaches have yet been tested in the field.

Mating disruption

It is likely that widespread dissemination of an aggregation pheromone throughout a crop will disrupt the formation of mating aggregations and prevent females from finding males. The approach has not yet been tested. One issue is that thrips are

haplodiploid and most have arrhenotokous reproduction in which fertilised eggs produce females and unfertilised eggs produce males. This means that even if mating is prevented, the females can still lay eggs, which will be male. Population reduction will not be seen until the second generation when a largely male population will produce very few offspring. Nevertheless, thrips generation times are very short and the effect could be seen within one crop season. Mass trapping with aggregation pheromone will disseminate the pheromone throughout the crop and may lead to mating disruption, so it is possible that some of the population reduction found in mass trapping trials is the result of mating disruption.

Mating disruption is hard to test rigorously. Experimental plots need to be very large, otherwise results are distorted by insects flying into the pheromone-treated plots, and this limits the amount of replication that is possible. However, in arrhenotokous thrips an increase in the proportion of males should be detectable if mating disruption is occurring.

Future research

Although we have now identified the aggregation pheromones of a few species of thrips, we still know very little about their role and how they work. As we understand more about them, we shall have a better idea of how best to exploit them for pest management. It is likely that their effects are more sophisticated than just attracting males and females from a distance. We need to understand the behavioural effects of the major and minor compounds and also how they interact with other pheromones.

Aggregation pheromones are in the process of being identified for several other species of pest thrips. Since pheromones can be part of species isolating mechanisms, they may be useful in indicating the presence of cryptic species. Evidence is growing that some thrips previously thought to be one species may actually be several species or sub-species (Rugman-Jones *et al.*, 2010; Hondelmann *et al.*, 2017; Gikonyo *et al.*, 2017), and these may turn out to have different pheromones.

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