CHEMICAL ECOLOGY OF THE THYSANOPTERA

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Abstract

The chemical ecology of the Thysanoptera is identified with a variety of natural products discharged in anal droplets during confrontations with adversaries. These exudates are fortified with defensive allomones that may function as repellents, contact irritants, or in some cases, fumigants. Thrips synthesize a large diversity of allomonal products that include hydrocarbons, acids, esters, aromatic compounds, and monoterpenes. Most of the exudates contain mixtures of natural products whose defensive efficacies may reflect synergistic interactions of selected compounds. That the anal secretions of thrips are highly effective repellents for a variety of ant species probably reflects the fact that formicids are the major predators against which these exocrine products have been evolved.

Introduction

Many species of thrips form dense aggregations that could constitute a bonanza for a variety of predators. In particular, ants would appear to be ideally suited to prey on thrips as a consequence of their ability to rapidly recruit large numbers of workers to good food finds. However, although thysanopterans are delicate insects, many species may be protected from predation by chemical defenses that are identified with anal discharges (Lewis 1973). Significantly, research in the last decade has demonstrated that many species of thrips are versatile natural-product chemists that biosynthesize a large variety of defensive allomones.

In the present report, the chemical ecology of thrips species is examined in terms of the chemistry of their defensive exudates. In addition, the roles of the compounds in the anal exudates are examined in terms of sympatric predatory species of ants. Hopefully, the elegance of thrips in blunting the attacks of very efficient predatory insects by utilizing chemical arsenals, will be clearly manifest.

Defensive Allomones of Thrips

Studies on the natural products generated by thysanopterans have been undertaken on species belonging to 12 genera (Tables 1-5). It appears that all identified compounds are present in anal discharges of species of Phlaeothripidae. In order to focus on the virtuosity of thrips as allomonal synthesizers, their natural products are fractionated into the major chemical classes to which they belong. The deterrent functions of these compounds are examined in the penultimate section.

Esters

Five aliphatic esters have been identified as natural products of thrips in five genera (Table 1). Included in this grouping are two lactones, Γ-decalactone and 4-octadec-9-enolide, which are also classified as cyclic esters.

Γ-Decalactone is distinctive in being one of two thrips defensive allomones that are in themselves the only compounds present in the secretions. This compound, a product of the Cuban laurel thrips, *Bagnalliella yuccae* (Hinds), is secreted by both adults and larvae, the former producing about twice as much as the latter (0.27 ± 0.15 vs. 0.12 ± 0.10 μg). No glandular cells could be identified with the synthesis of Γ-decalactone (Howard et al. 1983).

Two *Gynaikothrips* species, *G. ficorum* (Marchal) and *G. uzeli* (Zimmermann), produce three of the five esters characterized from thrips secretions (Table 1). Whereas tetradecyl acetate is a major allomone in *Varshneyia pasanii*, esters identified in the other species are minor constituents (Suzuki et al. 1988, 1989; Blum et al. 1988).

Table 1. Esters in thrips exocrine secretions

Compound	Occurrence	Authority
Γ-Decalactone	*Bagnalliella yuccae*	Howard et al. 1983
Tetradecyl acetate	*Gynaikothrips ficorum*	Howard et al. 1987
	Gynaikothrips uzeli	Suzuki et al. 1989
	Varshneyia pasanii	Suzuki et al. 1988
	Liothrips kuwanai	Suzuki et al. 1988
Hexadecyl acetate	*Gynaikothrips ficorum*	Howard et al. 1987
	Gynaikothrips uzeli	Suzuki et al. 1989
	Varshneyia pasanii	Suzuki et al. 1988
	Liothrips kuwanai	Suzuki et al. 1988
4-Octadec-9-enolide	*Euryaplothrips crassus*	Blum et al. 1988
Octadecyl acetate	*Gynaikothrips uzeli*	Suzuki et al. 1989

Aromatic Compounds

Four aromatic compounds have been detected in anal exudates of thrips in four genera (Table 2). Two compounds, phenol and phenylacetaldhyde, are minor concomitants of the major allomones that dominate the secretions of *Arrhenothrips ramakrishnae* and *Euryaplothrips crassus* (Blum et al. 1988).

Mellein, the only compound detectable in the exudate of *Haplothrips leucanthemi* (Schrank) (Blum et al. 1990), is a characteristic sex pheromone of male ants in the genus *Camponotus* (Brand et al. 1973). This anal product, which is an aromatic lactone, has also been identified in the defensive secretions of termite soldiers in the genus *Cornitermes* (Blum et al. 1982).

Juglone, a major constituent in the acid-rich secretion of *Elaphrothrips tuberculatus* (Hood) (Blum et al. 1987), is the only 1, 4-quinone identified as a thrips natural product. This quinone, a well-known allelopathic agent produced in walnut leaves (Rietveld 1983), is synthesized *de novo* by *E. tuberculatus* as the first example of the production of this compound by an animal.

Table 2. Aromatic compounds in thrips exocrine secretions

Compound	Occurrence	Authority
Phenol	*Arrhenothrips ramakrishnae*	Blum et al. 1988
	Euryaplothrips crassus	Blum et al. 1988
Phenyl-acetaldehyde	*Arrhenothrips ramakrishnae*	Blum et al. 1988
	Euryaplothrips crassus	Blum et al. 1988
Mellein	*Haplothrips leucanthemi*	Blum et al. 1990
Juglone	*Elaphrothrips tuberculatus*	Blum et al. 1987

Monoterpenes

The three monoterpenes identified as defensive allomones of thrips, have been detected as products of species in six genera (Table 3). Perillene, a furanomonoterpene produced by several ant species (Bernardi et al. 1967, Longhurst et al. 1979), has been characterized from the exudates of thrips in five of the six genera in which monoterpenes have been demonstrated to be present (Suzuki et al. 1988, Blum et al. 1988). This compound, which is generally present in admixture with several other compounds, varies in concentration from 23% in *Liothrips piperinus* to 2% in *Varshneyia pasanii* (Suzuki et al. 1986, 1988).

ß-Acaridial, a novel monoterpene only previously known as a product of a mold mite (Leal et al. 1989), is a major constituent in the anal exudates of all three species of thrips from which it has been identified (Table 3) (Suzuki et al. 1989). The function of this highly unstable dialdehyde is not known.

Rose furan, an isomer of perillene, is the major constituent in the secretion of *Arrhenothrips ramakrishnae* (Blum et al. 1988). It is accompanied by perillene in this exudate, along with two minor aromatic compounds (Table 2). *A. ramakrishnae* is the first animal demonstrated to synthesize this distinctive plant natural product.

Table 3. Monoterpenes in thrips exocrine secretions

Compound	Occurrence	Authority
ß-Acaridial	*Gynaikothrips uzeli*	Suzuki et al. 1989
	Varshneyia pasanii	Leal et al. 1989
	Liothrips kuwanai	Leal et al. 1989
Perillene	*Varshneyia pasanii*	Suzuki et al. 1986
	Liothrips kuwanai	Suzuki et al. 1988
	Liothrips piperinus	Suzuki et al. 1988
	Teuchothrips longus	Blum et al. 1988
	Arrhenothrips ramakrishnae	Blum et al. 1988
	Schedothrips sp.	Blum et al. 1988
Rose Furan	*Arrhenothrips ramakrishnae*	Blum et al. 1988

Hydrocarbons

Seven hydrocarbons fortify the anal exudates of thrips species in three genera (Table 4). Several of these compounds are always present in each secretion and they may constitute either major or minor allomones. For example, pentadecane is one of the two major compounds secreted by *G. ficorum*, whereas the other three alkanes are relatively minor constituents (Howard et al. 1987). Similarly, tridecane accounts for 66% of the secretion of *V. pasanii* whereas dodecane and tetradecane are trace constituents (Suzuki et al. 1986, 1988). It may be significant that all of these hydrocarbon producers are gall-inhabiting species.

V. pasanii is distinctive in producing six of the seven hydrocarbons identified in thrips anal exudates (Table 4) (Suzuki et al. 1986, 1988). However, all species in the genera *Varshneyia, Liothrips,* and *Gynaikothrips* produce a diversity of alkenes and/or alkanes, emphasizing that the members of these three taxa stress the production of allomonal hydrocarbons.

Table 4. Hydrocarbons in thrips exocrine secretions

Compound	Occurrence	Authority
Dodecane	*Varshneyia pasanii*	Suzuki et al. 1988
	Liothrips kuwanai	Suzuki et al. 1988
	Liothrips piperinus	Suzuki et al. 1988
Tridecane	*Gynaikothrips ficorum*	Howard et al. 1987
	Gynaikothrips uzeli	Suzuki et al. 1989
	Varshneyia pasanii	Suzuki et al. 1988
	Liothrips kuwanai	Suzuki et al. 1988
	Liothrips piperinus	Suzuki et al. 1988
Tetradecane	*Gynaikothrips ficorum*	Howard et al. 1987
	Gynaikothrips uzeli	Suzuki et al. 1988
	Varshneyia pasanii	Suzuki et al. 1988
(Z)-7-Pentadecene	*Varshneyia pasanii*	Suzuki et al. 1988
	Liothrips kuwanai	Suzuki et al. 1988
Pentadecane	*Gynaikothrips ficorum*	Howard et al. 1987
	Gynaikothrips uzeli	Suzuki et al. 1989
	Varshneyia pasanii	Suzuki et al. 1988
(Z)-8-Heptadecene	*Liothrips kuwanai*	Suzuki et al. 1988
	Varshneyia pasanii	Suzuki et al. 1988
	Gynaikothrips uzeli	Suzuki et al. 1989
Heptadecane	*Gynaikothrips ficorum*	Howard et al. 1987
	Gynaikothrips uzeli	Suzuki et al. 1989

Acids

Seven aliphatic acids have been characterized as natural products of thrips in four genera (Table 5). Two species, *Hoplothrips japonicus* and *Dinothrips* sp., are distinctive in producing anal exudates that each contain solely two acids (Table 5) (Haga et al. 1989, Blum et al. 1989). All the other thysanopterous species produce acids as either major or minor concomitants of other classes of defensive allomones.

For example, the anal discharge of *V. pasanii* is dominated by hydrocarbons and the single acidic constituent, 2-methylbutyric acid, a defensive product of swallowtail (*Papilio*) larvae (Eisner et al. 1965), is a trace constituent. On the other hand, the C_{12} and C_{14} acids fortifying the secretion of *E. tuberculatus* (Hood) (Table 5), are quantitatively significant constituents that accompany a 1,4-quinone (Table 2) (Blum et al. 1987). Similarly, decanoic and dodecanoic acids are the major constituents in the secretion of *Euryaplothrips crassus* and the aromatic and lactonic constituents (Tables 1 and 2) are minor products (Blum et al. 1988).

Table 5. Acids in thrips exocrine secretions

Compound	Occurrence	Authority
2-Methylbutyric acid	*Varshneyia pasanii*	Suzuki et al. 1988
Isovaleric acid	*Dinothrips* sp.	Blum et al. 1989
Decanoic acid	*Euryaplothrips crassus*	Blum et al. 1988
	Dinothrips sp.	Blum et al. 1989
(E)-3-Dodecenoic acid	*Hoplothrips japonicus*	Haga et al. 1989
(Z)-5-Dodecenoic acid	*Hoplothrips japonicus*	Haga et al. 1989
Dodecanoic acid	*Elaphrothrips tuberculatus*	Blum et al. 1987
	Euryaplothrips crassus	Blum et al. 1988
5,8-Tetradecadienoic acid	*Elaphrothrips tuberculatus*	Blum et al. 1987
(Z)-5-Tetradecenoic acid	*Elaphrothrips tuberculatus*	Blum et al. 1987

Roles of Exocrine Compounds

Although relatively few studies of the functions of thrips semiochemicals have been undertaken, it is evident that some of these compounds are defensive compounds against predatory insects such as ants. An examination of their main defensive roles clearly establishes their effectiveness as deterrent allomones.

Repellency

Γ-Decalactone, the only compound in the anal discharge of *B. yuccae*, repels workers of *Monomorium minimum* from entering treated tubes under both laboratory and field conditions (Howard et al. 1983). Similar results were obtained with workers of *M. pharaonis* and *I. humilis*. The offensive nature of this lactone for ants was further illustrated by its ability to induce workers (*M. minimum*) to deflect their antennae away from food sources on which they attempted to feed.

Suzuki et al. (1988) similarly reported that workers of *Pristomyrmex pungens* are repelled by the perillene-rich secretion of *V. pasanii*. This exudate also contains 2-methylbutyric acid, a known insect repellent (Eisner et al. 1965), and it is suggested that perillene may function as an alarm pheromone for *V. pasanii*. On the other hand, perillene was demonstrated to be a highly active repellent for workers of *M. minimum* and *I. humilis* under laboratory conditions (Blum et al. 1989).

Mellein, the only compound detected in the anal exudate of *H. leucanthemi*, is an effective repellent for hungry fire ant (*Solenopsis invicta*) workers (Blum et al. 1990). A dosage of 2 μg at a food source results in a significant reduction in the numbers of feeding workers.

The anal discharge of *G. ficorum* (4 thrips equivalents) deterred workers of the aggressive myrmicine ant, *Wasmannia auropunctata* (Howard et al. 1987). Treated filter papers, held 1 mm from feeding ants, reduced the number of ants at the bait by 60-80%, under field conditions.

Contact Activity

The deterrency of allomones in the anal secretions of thrips species appears to be considerable. Adults and larvae of *B. yuccae* apply their Γ-lactone-pure exudate to predatory ants with elongate setae that form a paint brush at the tip of the abdominal tube (Howard et al. 1983). Treated ant workers (*M. minimum*) quickly withdrew from the scene of the encounter, wiping exposed body parts on the substrate while exhibiting other grooming behaviors.

Similarly, the anal tube of *G. ficorum* bears several spines that function as an effective brush for transferring the anal exudate to attacking ants (*W. auropunctata*) (Howard et al. 1987). Significantly, thrips are able to resorb unused anal droplets back into the rectum, thus conserving this important defensive secretion. Treated ant workers withdrew from the scene of the encounter, flattening against the substrate while dragging themselves forward. Ants frequently bit at the substrate and were sometimes attacked by sister workers. In addition, the thrips secretion appears to also function as a distracting adhesive, with debris frequently adhering to the cuticle of treated workers.

Both hexadecyl acetate and pentadecane, the major constituents in the secretion of *G. ficorum*, induced typical dragging behavior in ant workers after topical administration (1 thrips equivalent) (Howard et al. 1987). The ester was more active than the alkane, but a mixture of the two compounds was considerably more active then either compound alone at equivalent concentrations, indicating that the two allomones were interacting synergistically.

Mellein, the single defensive allomone produced by *H. leucanthemi*, has previously been demonstrated to be an excellent contact deterrent for ant workers (Blum et al. 1982).

Conclusions

The Thysanoptera would appear to constitute a veritable cornucopia of interesting exocrine compounds. Although the chemistry of only 14 species has been investigated, nearly 30 compounds have already been identified (Tables 1-5). Natural products such as Γ-decalactone, juglone, and rose furan constitute new animal natural products, and ß-acaridial has not previously been detected in insects. Considering how few thrips species have been chemically analyzed, it will not prove surprising if subsequent investigations provide additional evidence for the biosynthetic virtuosity of these insects.

The deterrent efficacies of the thrips allomones provide grounds for considering these insects as an excellent source of new insect repellents. These compounds have been "tried and tested" in evolutionary time, and obviously provide their producers with the chemical arsenals needed to blunt the attacks of omnipresent aggressors such as ants. In the case of aggregative species of thrips, communal living enables them to pool their allomonal resources in order to challenge predators with an emphatic message of deterrency (Howard et al. 1983). In addition, it seems likely that gall-inhabiting species, living in confined environments, may utilize their defensive exudates in a fumigatory capacity as well (Howard et al. 1987).

Finally, it has been suggested that perillene, a product of *V. pasanii*, functions as an alarm pheromone (Suzuki et al. 1988), and similarly, (*E*)-3-dodecenoic acid, a product of *H. japonicus*, is believed to be an alarm and/or aggregation pheromone (Haga et al. 1989). Pheromones may be widespread in the Thysanoptera, an order that is characterized by a large number of aggregative species. Considering the fact that many species of thrips are of considerable economic importance, this possibility should act as a spur for analyzing the chemical ecology of these insects in great depth. And the sooner the better!

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Discussion Period

Question: How do you handle thrips for extraction purposes?

Blum: There are two ways. One way is simply to pickle them in a special solvent. Another way is to collect droplets secreted directly from the thrips. Some interesting volatile compounds are secreted in these droplets. We collect the droplets from the thrips on a slit of filter paper under a microscope and add a little of the solvent and then analyze it. We only need about 5 or 10 thrips when we treat them that way. With this method, you can pin down the source of the compounds. As I indicated before, we currently have no idea where these compounds are made but they do accumulate in the hind gut.

Question: Do the chemicals come from the host plants?

Blum: No. We haven't found any correlation whatsoever. We have investigated numerous thrips species that feed on fungi. We have also analyzed the fungi but have not found any of the thrips compounds in the fungi. These little insects are marvelous chemists in their own right and I want to give them all the credit they deserve. Though our findings indicate that they are making the compounds, this does not mean that we won't encounter species that do use compounds found in plants. If you work with enough insect species you are bound to find exceptions to the rules. I have a friend who studied chemical defenses in beetles and he thought he had everything worked out until he looked at one more species. This species was not making any of the typical defensive compounds. Instead, it was sequestering plant compounds and then secreting them for its own defense. I'm sure we will find this in a thrips sooner or later, but currently we have no evidence that the thrips are not making the compounds themselves.

Question: What about looking at precursors of the compounds in the fungi?

Blum: One could do that, but it would be a very difficult task. It depends on how far back you want to go. A friend of mine is a fungal chemist and I try to keep up with what he and his colleagues are doing. The fungi are absolutely bizarre in what they synthesize so I would hate to get involved in trying to analyze fungal chemicals. Fungi do things that seem to make no sense. You can obtain from fungi everything from psychedelic compounds to some of the most deadly poisons in the world. These fungal products are very complex molecules.

Question: The examples you've shown are of thrips producing defensive chemicals. Have you ever heard of a thrips producing a chemical that was attractive?

Blum: You've raised a very good question. I feel that I've given you a very inadequate picture in most cases of what we have done. We obtain the material from thrips, and that is often a one shot thing. We may get eight vials of the extracts and then we do the bioassays in our laboratory on the defensive potential of the compounds against ants. Ants may not be the most appropriate insect to work with but we feel these compounds have to be taken back into the context where these thrips are and where they are interacting with other organisms. This is almost never done. A Japanese study is the only other one that tried a similar approach. Based on their bioassays, they believed that the compound was an alarm pheromone, but we've isolated the same compound from another thrips species and it's a very good repellent. It was previously known to be an excellent repellent for insects. However, with the thrips species we worked on, it shows no dispersing activity.

What we need is a collaboration between those working with a particular thrips species and those doing the chemical extraction and analysis. As the saying goes, you must know your enemy (or your friend) and research is desperately needed to increase our knowledge about thrips so that sensitive and complex studies can be conducted. These studies haven't been done. I believe that many of the compounds that we have worked on may have multiple functions, but we don't have the field work to confirm this hypothesis. More chemical, behavioral and biological collaboration is needed in this field. Many thrips species produce obvious anal exudates which need to be analyzed so that they can be made available for behavioral and ecological studies.

Question: Do you think these secretions are more common in social species than in those that live independently?

Blum: I don't know. Right now we are at the very beginning of understanding the chemical ecology of thrips and almost anything that we can do now is a sizable contribution to a very limited base of knowledge. There are almost no data on this topic.

Question: Have you looked at the volatility of these compounds?

Blum: I believe that some of the compounds that thrips give off are functioning as fumigants. For example, some are given off in plant galls and I think they would effectively repel potential predators. Most of these compounds are very stable.

In contrast, the compound produced by an African species isn't so stable. However, once it hits a predator's antennae, that predator will probably not be able to smell for some time because the compound may immobilize olfactory proteins. The predator will have to synthesize new proteins to reactivate its sense of smell. Remember, any time you have a system that blunts the olfactory system of a predator that is dependent on olfaction, that predator is essentially blind, even when it is right beside its prey. These compounds are really good repellents in that sense. I have the feeling also that thrips may be beating the ants at their own game because of the congruency of thrips defensive compounds and ant compounds. The same compounds occur over and over again, which makes me think the thrips may be chemically mimicking the ants, thereby driving them into a dispersing frenzy with the compounds that the ants normally utilize for the same function.

Question: We have noticed in the field that some people seem to attract more thrips than other people. Do you have any clues as to why this occurs?

Blum: Of course this is something that always intrigues entomologists. We all know that mosquitoes attack some people more than others. One person may be very attractive to mosquitoes whereas another person may not be attractive at all. I think the answer is partly related to the odorants and other compounds that we put on our bodies. Many of these compounds are identical or very similar to natural products produced by insects and other animals and cause them to react accordingly.

I'll give you a example. We were in downtown Washington, D.C. with our daughters and they wanted popsicles. Each one got an orange popsicle and as we walked along they were suddenly engulfed with a swarm of honey bees. The attraction was very strong. I felt this was not coincidence, there had to be something volatile in the popsicles that was stimulating the bees. Four years later scientists at Agriculture Canada in Ottawa found that citral, an ingredient in orange popsicles, was produced in a gland on the abdomen of the honey bee workers, and that in large quantities it was a strong attractant for honey bees. My point is that compounds like this may be put into fragrances and polishes, and these compounds may sometimes be identical to pheromones which insects produce.