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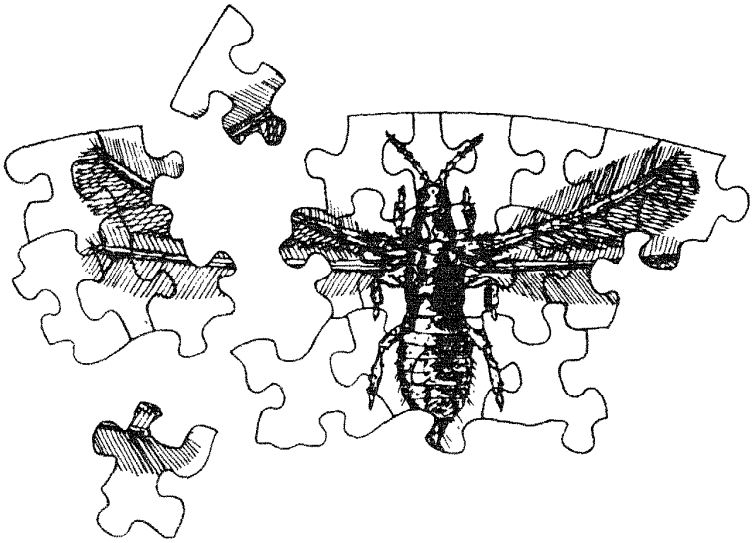
Towards Understanding Thysanoptera



Editors:

Bruce L. Parker
Margaret Skinner
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TOWARDS UNDERSTANDING THYSANOPTERA

TOWARDS UNDERSTANDING THYSANOPTER

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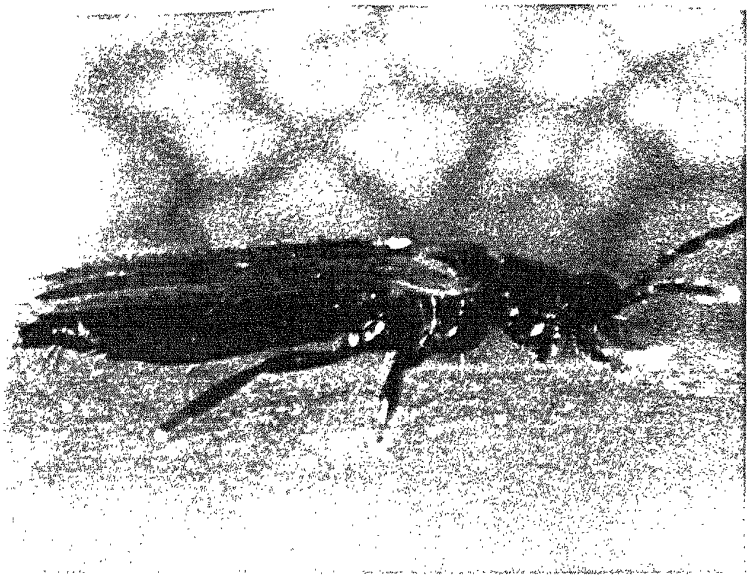
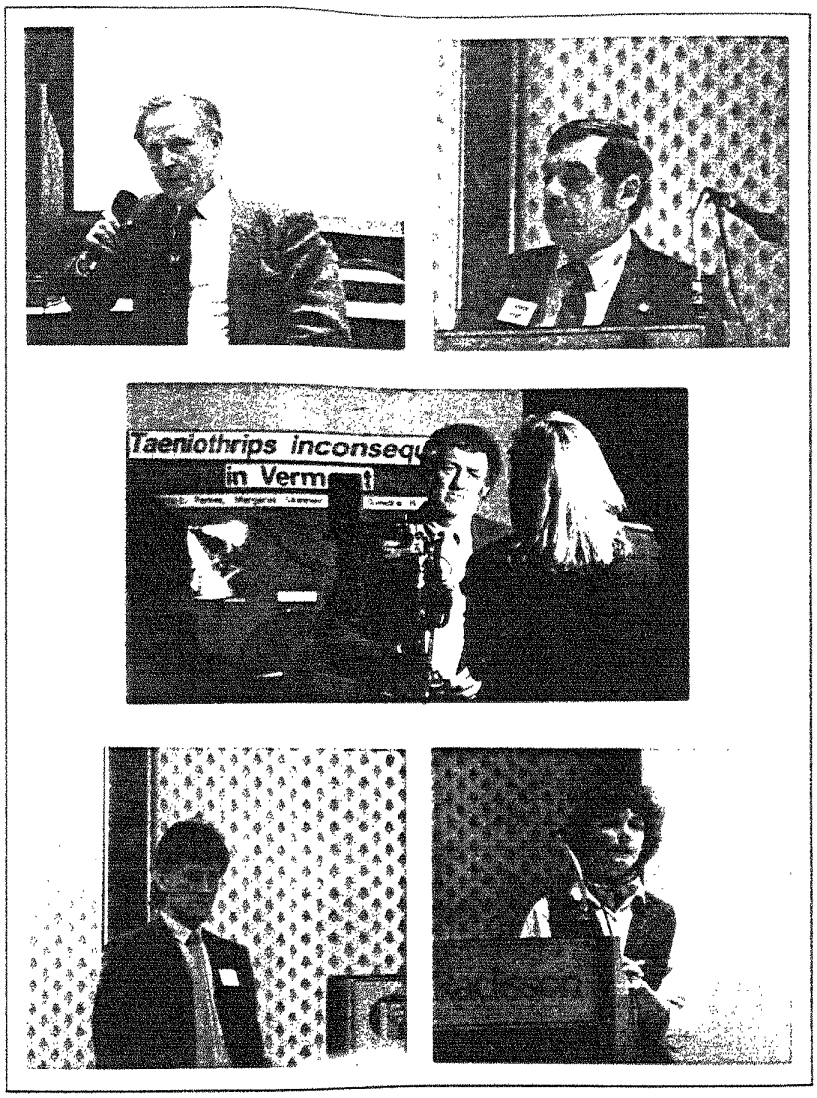


PEAR THRIPS, *Taeniothrips inconsequens* (Uzel)
(photo by T. E. Downer)



A few of the conference participants (from top left to bottom right): Trevor Lewis, Institute of Arable Crops Research; Conrad Motyka, VT Department of Forests, Parks and Recreation; Bruce L. Parker, The University of Vermont; Nick J. Mills, Commonwealth Institute of Biological Control; Margaret Skinner, The University of Vermont.

PREFACE

Pear thrips, *Taeniothrips inconsequens (Uzel)*, first surfaced as a pest of sugar maple, *Acer saccharum* Marsh, in Pennsylvania in the late 1970s. Though similar damage was observed in Vermont in the early 1980s, it was probably misdiagnosed as frost damage until 1985, when finally thrips were positively confirmed as the causal agent. Pear thrips damage to sugar maple fluctuated greatly from year to year, raising only slight concern among sugarmakers and forest managers. However, the situation changed dramatically in the spring of 1988, when pear thrips caused widespread, severe foliage damage to sugar maple in southern Vermont (over 200 thousand hectares) and other New England States. Recognized as a potential threat to forest health, pear thrips received tremendous media coverage, including the front page of the New York Times and the CBS Evening News!

The response in Vermont to this crisis was swift. With support from the Vermont legislature and the Department of Agriculture, a major research effort was launched, coordinated jointly by the University of Vermont and the VT Department of Forests, Parks and Recreation. This pest presented unique research and management challenges. Pear thrips on sugar maple represented a known pest on a new host in a new habitat. As of 1988 almost no information existed on this insect in a sugar maple forest. In addition thrips in general were virtually unknown as a northern hardwood forest pest, and forest managers knew little about how to handle such an insect. Finally, because thrips are such small insects, new and specialized methods were needed for survey and study of this pest.

As Vermont's research efforts got underway, it became clear that much could be learned from scientists familiar with other thrips species. The goal of this conference was to gather these specialists together to present their ideas on thrips survey and management methodology, particularly as it related to pear thrips in a forest setting. Participants came from across the United States, Canada and the United Kingdom to share their expertise. Though many didn't know that a "sugarbush" was not a shrub, but a natural stand of mature 30-m-tall sugar maple trees (100 ft), they all knew what maple syrup was! Certainly by the end of the conference all of the participants recognized the unique value of the sugar maple to the heritage and economy of Vermont and the Northeast, and shared our concern for its future in light of the threat of pear thrips.

We thank all of the conference participants who freely and enthusiastically shared their knowledge. Without their expertise and continued technical support, our pear thrips research would not have progressed as far or as fast as it has. We thank all those attending the conference for helping to make it a productive event. Though the pear thrips problem is far from being "solved," this conference started the research process on a solid footing.

BEHAVIOR AND BIOECOLOGY

FEEDING, FLIGHT AND DISPERSAL IN THRIPS

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Introduction

The aim of this paper is to amplify some of the general points made in my introductory paper on the order Thysanoptera (Lewis 1990, this proceedings), with particular reference to feeding, flight and dispersal. These aspects of thrips behaviour are clearly of great relevance to the spread and effects of infestations of *Taeniothrips inconsequens* in New England, and although most of the work described has concentrated on another species, *Limothrips cerealium* (Haliday) (Lewis 1973, Chisholm & Lewis 1984) much of the information is probably applicable to terebrantian species of similar phytophagous habits and size such as the pear thrips.

Feeding

During feeding on stem, leaf or flower sap, adult and larval thrips adopt a characteristic stance with the tip of the mouthcone pressed on to the substrate surface with which close contact is maintained by means of the labial pad (see p. 5, Fig. 1). The maxillary and labial palps are spread out on each side and just touch the substrate, presumably to provide sensory information (Fig. 1). Other hairs and sensillae on the front of the head and paraglossae, respectively, probably have a tactile and chemosensory function. When the insect is not feeding, the labral pad is withdrawn and covered by the paraglossa. As the thrips explores a feeding site these move aside to expose the horseshoe-shaped labral pad which rapidly unfolds to its full size as it is pressed against the substrate.

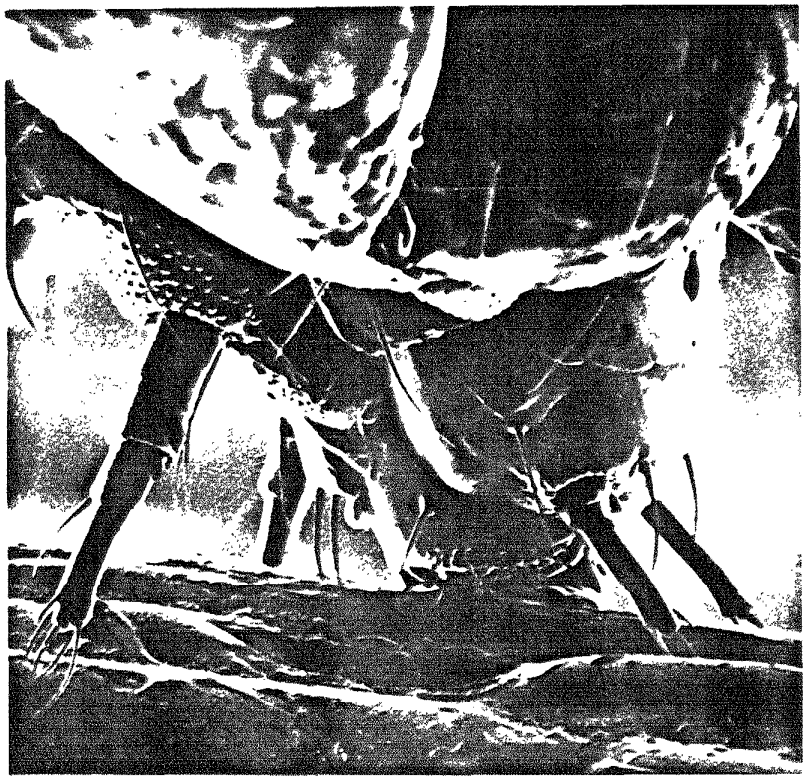

Figure 1. Side view of mouthcone of feeding *Limothrips*; maxillary palps (left) and labial palps (right) sense the leaf surface; the labral pad and paraglossal sensilla are pressed closely against it (x250).

The mandible is stout with a broad base apparently fused to the internal ridge marking the junction between frons and clypeus. In fact, it is articulated to this thickening at one point only, so as to make an initial opening in plant tissue. The whole head capsule, with the mouthcone serving as pivot, is thrust downwards and slightly backwards, then the mouthcone shortens, forcing the mandible to protrude about 20 μ and rupture the epidermis of the plant tissue. The final penetrative stab is usually preceded by a series of less powerful exploratory thrusts.

Once the plant epidermis is pierced the mandible is largely withdrawn and the two styliform maxillae are inserted as a unit up to 60 μ into the underlying cells. The two stylets can move independently, but because ridges on the right stylet fit into grooves bordering the left stylet they function jointly as an efficient tube through which cell contents are imbibed.

Cinematographic pictures of feeding (Chisholm & Doncaster 1982) show inflow confined to the end of the tube, but liquid can be taken through a sub-terminal orifice even when one stylet is extended a shorter distance than the other.

Muscular pulsations at 2-6/sec are visible through the pale head capsule of larvae, and the resulting pumping action draws in liquid and chloroplasts from the plant. The internal diameter of the maxillary tube in *L. cerealium* is only about 1 μm, far smaller than wheat protoplasts. However, the thrips easily pierce the plasmalemma enclosing each protoplast with their maxillae, gaining access to the chloroplasts. Even when these greatly exceed the diameter of the maxillary tube, the suction created by the muscular pumping is sufficient to distort them enough to allow their passage up the tube. This species appears able to ingest about 8.5×10^{-5} μl/min which equates to about 12.5% of its body weight per hour.

By contrast Day & Irzykiewicz (1954) estimated that *Thrips tabaci* Lindeman, a smaller species than either *L. cerealium* or *Taeniothrips inconsequens* imbibed about 17% of its body weight per hour; 10-20% would seem a likely average consumption for phytophagous Terebrantia.

The effects of stylet penetration by *Limothrips* are easily detectable microscopically on the surface and within leaves. Externally, probing sites are visible because the presence of the labral pad removes surface wax, and the leaf cuticle so exposed often wrinkles, indicating plasmolysis in the epidermal cells. Sometimes a "silvered" patch develops under an area of concentrated punctures as air penetrates the emptied plant cells. Many of the holes remaining after the stylets have pierced the leaf are approximately "figure-of-8"-shaped, presumably produced by the mandible and maxillae, though the extent to which this shape is attributable to probing or subsequent wrinkling of the substrate is uncertain (see p. 13, Fig. 2).

Within leaves, there is little sign of seepage of cell contents after feeding, indicating that the cells below the puncture are completely emptied. These empty cells are clearly visible, even where feeding has been light and where no surface silvering is visible. Emptied cells usually lie beneath a collapsed epidermal cell, and their appearance is the same whether the upper or lower epidermis has been pierced.

After more extensive feeding, when the plant tissue shows obvious external signs of damage, including widespread silvering, the internal cell structure is completely disrupted, the epidermal cells, especially the bulliform cells become shrivelled and distorted, a sign of extreme desiccation (Esau 1961). Many of the mesophyll cells disappear completely, others retain no cytoplasm or cell contents, and those that do show extreme plasmolysis with the cytoplasm contracting from the cell walls and deformed chloroplasts. The epidermal cells often collapse completely, with visible wrinkling of the outer cuticle. Cytoplasm contracts away from mesophyll cell walls which become flaccid. These effects are not directly attributable to feeding but flow from desiccation of the pierced and surrounding cells.

The effects of leaf-feeding by other terebrantian thrips on other crops can be much more obvious and serious. Heavily infested leaves of all ages shrivel, become discolored and brittle, and eventually fall, especially in hot, dry weather (Lewis 1973). To the extent that many of these harmful species, including *T. inconsequens*, are of a similar size to *L. cerealium* with mouthparts likely to penetrate to similar depths, the effects of feeding on leaves by thrips described above probably apply to most leaf-feeding species in the sub-order.

Flight and Dispersal

Thrips are among the weakest flying insects, yet their finely fringed wings enable them to remain airborne long enough for the wind to blow them to great heights and for long distances. Indeed, migration by flight from breeding sites is a regular event in the life cycle of many species. Although it produces widespread scattering, resulting in the loss of millions of individuals, it nevertheless ensures that fresh food is found for breeding populations, and sheltered sites for protection during unfavorable seasons.

The upper limit to which thrips are carried is unknown but, in Louisiana, using sticky traps fitted to aircraft, Glick (1939) caught one *Frankliniella tritici* (Fitch) and one *Haplothrips graminis* Hood above 3,100 m (10,000 ft) and 89 specimens representing at least 16 species at lower altitudes above 6 m (20 ft). At Darango, Mexico, *Stomatothrips flavus* Hood and *Caliothrips phaseola* Hood were caught at 1,200 m (4,000 ft). An interesting and surprising feature of the data from Louisiana is the number of thrips caught at night, representing 35% of the total when catches from 150 m (500 ft) are included. Five out of the six night-flying individuals caught by Glick were at 150 m, but a *Sericothrips* sp. was caught at over 1,500 m (5,000 ft). Night flight can prolong the migration of other insects, for example aphids (Berry & Taylor 1968), and small insects may often fly at night in continental regions where warm, low-level jet streams develop above nocturnal inversions enabling individuals carried upwards earlier in the day to remain airborne during darkness.

There are a few indications that the migration of some thrips species over large continental land masses might be associated with frontal winds. In the United States *F. tritici* may be blown northwards every year. It has never been recorded hibernating in Illinois, yet large numbers of this species appear suddenly in spring (Stannard 1968), and similarly in Maryland it was suddenly abundant in June, 1957 (Henneberry et al. 1961). In view of the major displacements of leaf hoppers, bugs and aphids by large-scale weather systems in North America, it seems probable that flying thrips could likewise be carried by frontal winds.

Notwithstanding Glick's (1939) records, most flight usually occurs during the warmest period of the day (Lewis 1973) so the insects are airborne when ascending convective movement is greatest and many are blown upwards and away from their breeding or overwintering sites. Tree-dwelling species or those emerging from the ground beneath a tree canopy, as is the case with pear thrips in a sugarbush, may represent a special case in that the emerging population in spring is subject to less convective air movement than populations emerging in more exposed habitats. Nevertheless, it would be surprising if there were not some significant movement of such species over long distances, particularly of individuals from the edges of the stands, and trapping with suction and/or sticky traps (Lewis 1973) at different distances from sugarbushes should resolve this question. Important details of the design and placement of traps and interpretation of trap catches are given by Lewis (1973). White traps are known to be particularly attractive to several species of *Taeniothrips* (Lewis 1961). Vertical profiles of aerial density, corrected as appropriate for wind speed at different altitudes (Johnson 1957, Lewis 1959, 1964) would also indicate the propensity of pear thrips to disperse long distances. Concentrations of pear thrips populations around the edges of sugar maple stands may occur if individuals are widely distributed by aerial currents, as is the case with *Taeniothrips laricivorous* Kratochvil on the edges of larch stands (Zenther-Møller 1965).

Some species are renowned for "mass" flights, usually occurring when populations build up on host plants, then take off in response to favorable weather (Lewis 1964, 1965). In England some species of *Taeniothrips* behave in this way. A careful study of the effect of weather on mass flights of *L. cerealium* in southern England (Hurst 1964, Lewis 1964) showed that six meteorological criteria were likely to pertain. These were: no rain or drizzle during the day, maximum temperature at least 20°C, day mean temperature above that of the previous day, low dry adiabatic lapse rate with no convection above about 1,600 m (5,000 ft), at least 1 h of sunshine, and dew point between 5 and 15°C. However, *Taeniothrips* spp. were among those that did not always conform to these criteria, and they sometimes flew in more humid and cooler conditions. A study of the flight habits of *Taeniothrips inconsequens* in New England in relation to weather would therefore be a novel and probably rewarding exercise.

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STRUCTURE OF THE MOUTHPARTS OF *Frankliniella bispinosa* (Morgan) (THYSANOPTERA: THRIPIDAE)

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Introduction

Thrips are increasingly recognized as potentially serious pests in a number of different agricultural, ornamental and sylvan commodities worldwide as indicated by the papers presented at this conference. The small size of thrips, their large numbers, capacity for flight and wind dispersal, wide host ranges, poorly understood life histories and probable potential for pesticide resistance exacerbate the timely development of control strategies. Thrips feed on pollen, leaves, flowers or young fruit and oviposit in various plant tissues. Some thrips feed on other arthropods or on fungal spores or hyphae. Plant injury is characterized by chlorosis, distortion or galling of leaves, spotting of leaves or fruit with fecal droplets, scarring of young fruit, premature fruit loss, or reduced yields from excessive reduction by feeding in the quality or quantity of viable pollen (Palmer et al. 1989). Several thrips species also function as direct or indirect vectors of certain viral, fungal or bacterial diseases (Ananthakrishnan 1980). These problems focus on the need for a better understanding of thrips including the structure and function of their mouthparts relative to plant injury and disease transmission.

Studies by Mound (1971), Heming (1978), Milne & Manicom (1978), Chisholm & Lewis (1984) and others have conclusively shown that thrips have piercing-sucking mouthparts. Excellent morphological studies of a limited number of thrips species have been completed including the larvae of *Haplothrips verbasci* Osborn by Heming (1978), *Limothrips cerealium* (Haliday) by Chisholm & Lewis (1984), *Scirtothrips citri* (Moulton) by Wiesenborn & Morse (1988), *Frankliniella occidentalis* (Pergande) and *F. schultzei* (Trybom) by Hunter & Ullman (1989).

Thirteen species of thrips have been identified in association with citrus flowers and developing buds in Florida with *Frankliniella bispinosa* (Morgan) the prevalent species (Childers et al. 1990). Injury to citrus flowers and buds by *F. bispinosa* has been documented (C.C.C. & D.S.A, unpublished data). Chemical control programs are in progress to evaluate the impact on fruit set following suppression of thrips during the citrus flowering cycle.

The object of this paper is to review the structure of the mouthparts of *F. bispinosa* illustrated by a series of light, scanning and transmission electron micrographs. This will provide additional information to identify or compare structures with those of other species of thrips.

Materials and Methods

At frequent intervals between February and April 1988, thrips were collected from open flowers or swollen buds in a "naval" orange grove directly into one pint or one quart Mason jars filled with 70% ethanol and returned to the laboratory. Open flowers and swollen buds with live thrips were collected directly into paper bags in the field, placed in an ice chest and returned to the laboratory for processing.

Light Microscopy. Whole-mounts of thrips were prepared using Hoyer's mounting medium (Krantz 1978). Light micrographs were taken through a Zeiss compound microscope equipped with a Minolta 35mm camera on Panatomic X ASA 32 film.

Scanning Electron Microscopy (SEM). Chloroform was applied directly to the blossom on which selected individual thrips were feeding in the laboratory. Dead or inactive thrips were then transferred into micro-tissue capsule tubes enclosed by 150 mesh grids and placed in 3% glutaraldehyde or Hallam's variation of Karnovsky's fixative with a 0.1 M potassium phosphate buffer at pH 7.2 for 3-4 hr (Hallam & Chambers 1970). Post-fixation was in 2% osmium tetroxide in the same buffer for 4 hr at 25°C. Samples were dehydrated in ethanol and critical point dried in a Ladd Critical Point Drier using carbon dioxide. Thrips were mounted ventral side up on stubs, sputter coated with 150-200 Å gold in a Ladd Sputter Coater and examined and photographed with a Hitachi S530 Scanning Electron Microscope.

Transmission Electron Microscopy (TEM). Individual thrips were fixed as above, dehydrated in acetone and embedded in Spurr's plastic (Spurr 1969). Gold and silver sections made on an LKB Huxley Ultramicrotome were stained with methanolic uranyl acetate (Stempack & Ward 1964) for 15 minutes and post-stained with lead citrate (Reynolds 1963) for five minutes. Grids were examined with a Philips 201 electron microscope. For light microscopy, one micrometer transverse sections of embedded thrips mouthparts were prepared using glass knives. Each section was collected and counted from the first identification of stylets. Sections were stained with 0.1% toluidine blue before observation (O'Brien et al. 1964).

Results and Discussion

Numerous setae are evident on the frons (f) and genal (g) areas of the head and mouthcone of *F. bispinosa* (Fig. 1) while the clypeus (c) is free of setae. The mouthcone of *F. bispinosa* is typical for terebrantian thrips and is characterized by the presence of the labrum (lm) in front, two distally tapered lobes, the maxillary stipites (ms), that form the sides of the mouthcone and the labium (=prementum (pm) and postmentum (psm)) behind (Heming 1978) (Figs. 1, 2). The mouthcone is about 130 μm long in the adult female *F. bispinosa*, is situated towards the basal end of the head capsule, and projects ventrally between the prothoracic legs (Fig. 2).

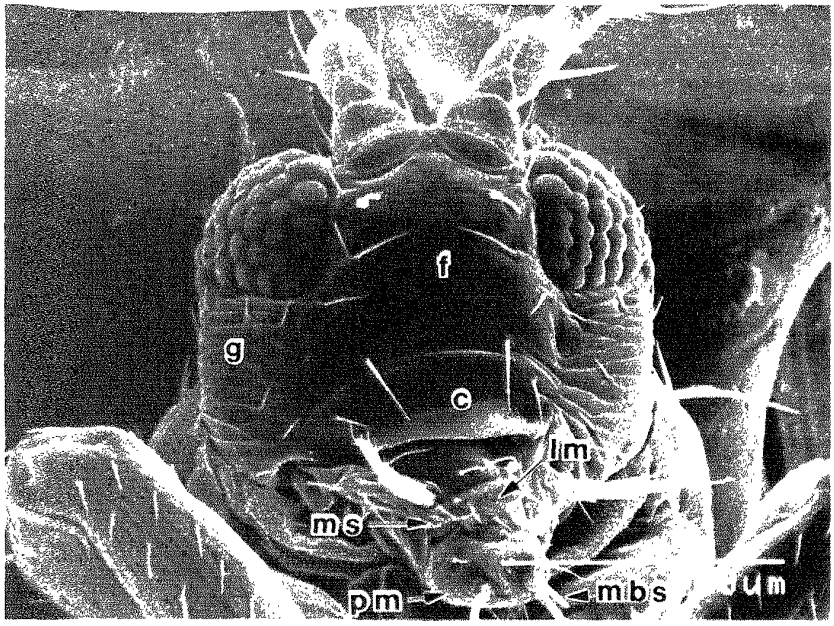

Figure 1. Scanning electron micrograph (SEM) of the head capsule of an adult female of *F. bispinosa* showing: (g) gena, (f) frons, and (c) clypeus. Mouthcone showing: (lm) labrum, (ms) maxillary stipes, (pm) prementum and protruding (mbs) mandibular stylet.

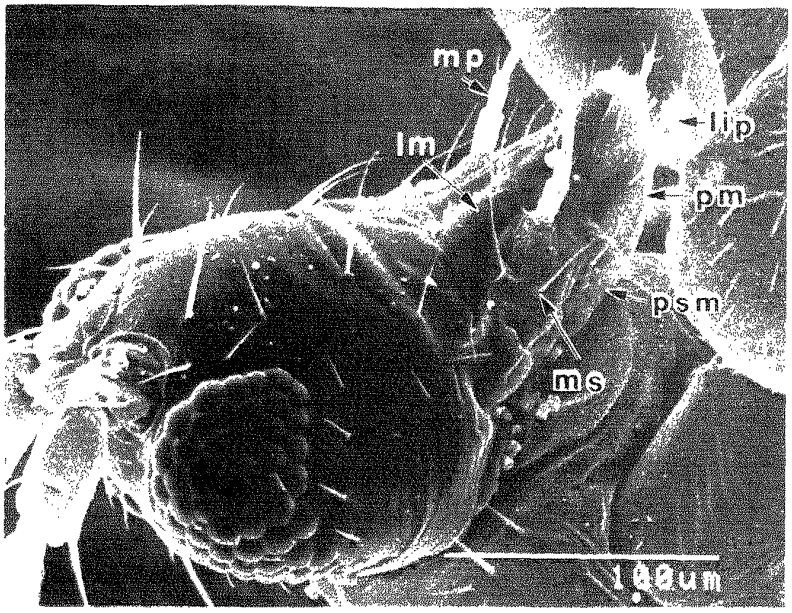

Figure 2. SEM of the lateral aspect of head capsule showing: (ms) maxillary stipes, (pm) prementum, (psm) postmentum, (lip) labial palp, (lm) labrum and (mp) maxillary palp.

The principal feeding structures contained within the mouthcone resemble those of hemipterans and consist of cibarial and salivary pumps, and elongate hypopharynx, two maxillary stylets and the left mandibular stylet (Heming 1978). Thrips differ from hemipterans in having maxillary and labial palpi, lacking both mandibular plates and a salivary canal between their protracted maxillary stylets and in having only the left mandibular stylet (Heming 1978).

The larger maxillary palpi (mp) are inserted into the maxillary stipites (ms) about midway down the mouthcone while the smaller, labial palpi (lip) are at the tip of the prementum (pm) (Fig. 2). Located at the distal end of the mouthcone are two paraglossae (pg) (Fig. 3). When a thrips is not feeding, the paraglossae press against each other providing a protective cover over the tip of the mouthcone. Each paraglossa bears a series of three morphologically distinct types of sensilla comprising (1) sensilla basiconica without a distinct cuticular collar (sbo) (2) sensilla basiconica with a distinct cuticular collar (sbc) and (3) sensilla trichodea (st) (Figs. 3, 4) (Richards & Davis 1977, Chisholm & Lewis 1984). Hunter & Ullman (1989) demonstrated that these sensory pegs are innervated. Their position and proximity to the feeding site suggest an olfactory and gustatory function (Chisholm & Lewis 1984). Arrangement, number and type of sensory pegs in females of *F. bispinosa* are similar to those of *F. occidentalis* (Hunter & Ullman 1989). However, Chisholm & Lewis (1984) reported only nine individual sensilla on each paraglossa of *Limothrips cerealium*.

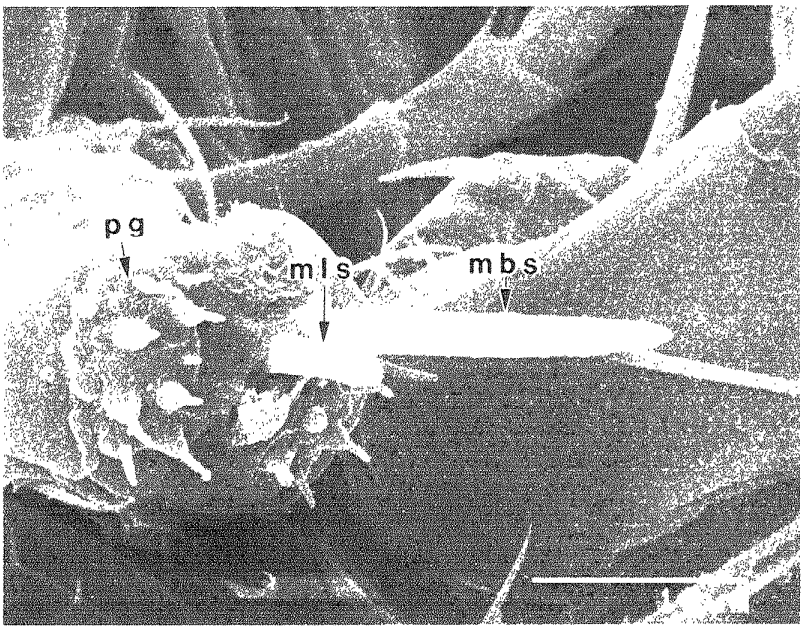

Figure 3. SEM of the tip of mouthcone showing: (pg) paraglossa with sensory pegs, (mls) paired maxillary stylets and (mbs) single mandibular stylet.

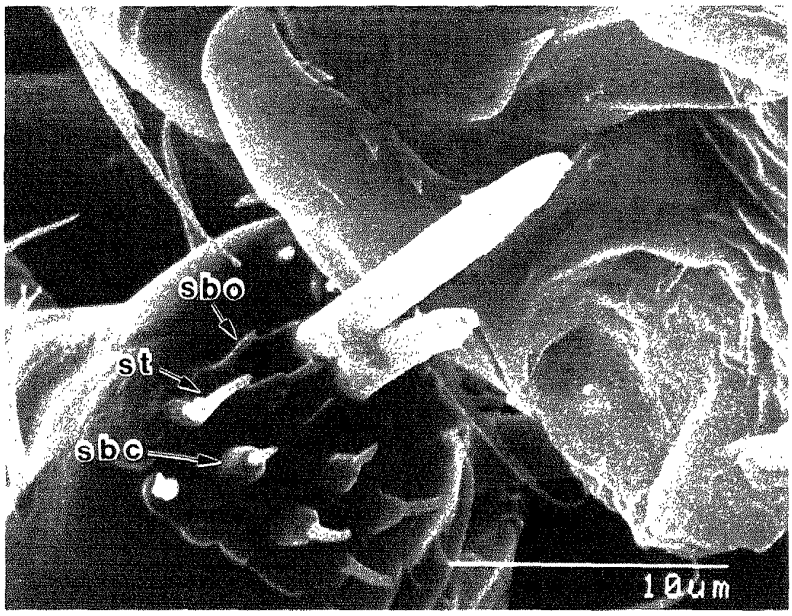

Figure 4. SEM of the mouthcone showing paraglossa with: (sbo) sensillum basiconicum without a distinct cuticular collar, (sbc) sensillum basiconicum with a distinct cuticular collar and (st) sensilla trichodeum.

When the paraglossae open laterally, they expose the ventral surface of a horse-shoe shaped labral pad (lp) bearing elongate papillae about its dorsal and lateral margins (Figs. 5, 6, 7). A second set of more slender papillae (p) are situated along the ventral edge of the pad. The function of these papillae is not known (Chisholm & Lewis 1984). The labral pad of *F. bispinosa* females is around 11 μm across.

A thrips presses the tip of its mouthcone against the plant substrate in preparation for feeding. This close contact is maintained by means of the labral pad. According to Chisholm & Lewis (1984) the only function presently attributed to the labral pad is to support the slim maxillary stylets as they are protracted into plant tissue. Thrips use the single mandible to make an initial opening by punching through the plant cuticle before feeding. Entry is achieved by a characteristic rocking of the head and a forceful downward and backward thrusting of the head capsule (Chisholm & Lewis 1984).

Based on studies by Heming (1978), the mandible is capable of only limited movement due to its orientation, musculature and articulation within the head capsule. He indicated that maximum protraction of the mandible is about one-third of its length. Chisholm & Lewis (1984) found that adult females of *L. cerealium* never extended the mandible beyond 20 μm even though its overall length was 102 μm. Maximum observed protraction of the mandibular stylet was 41 μm for one *F. bispinosa* adult exposed to chloroform while feeding (Figs. 8, 9). The mandibular stylet lacks an opening or food channel and is used principally to punch a hole in the substrate followed by insertion of the paired, tongue-in-grooved maxillary stylets (Fig. 10).

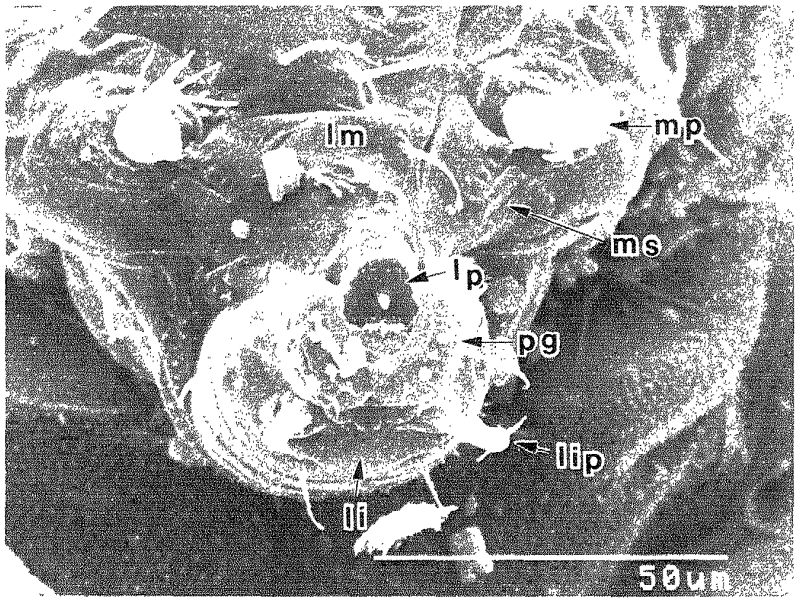

Figure 5. SEM of the frontal aspect of mouthcone showing: (lm) labrum, (mp) maxillary palp, (ms) maxillary stipes, (lp) labral pad, (pg) paraglossa, (lip) labial palp and (li) labium.

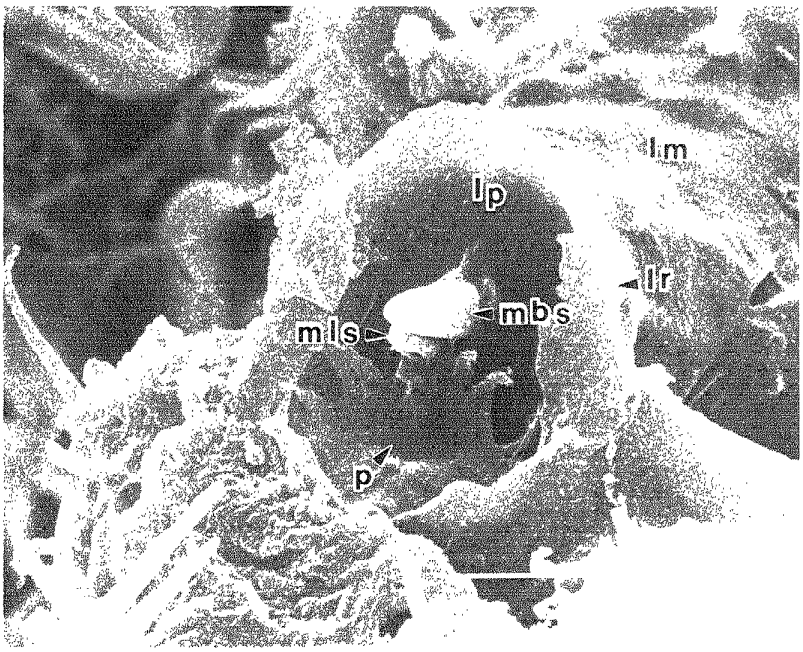

Figure 6. SEM of tip of mouthcone showing: (lm) labrum, (lp) labral pad, (lr) ring of papillae, (mbs) tip of mandibular stylet, (mls) paired maxillary stylets and (p) ventral papillae associated with part of glossa.

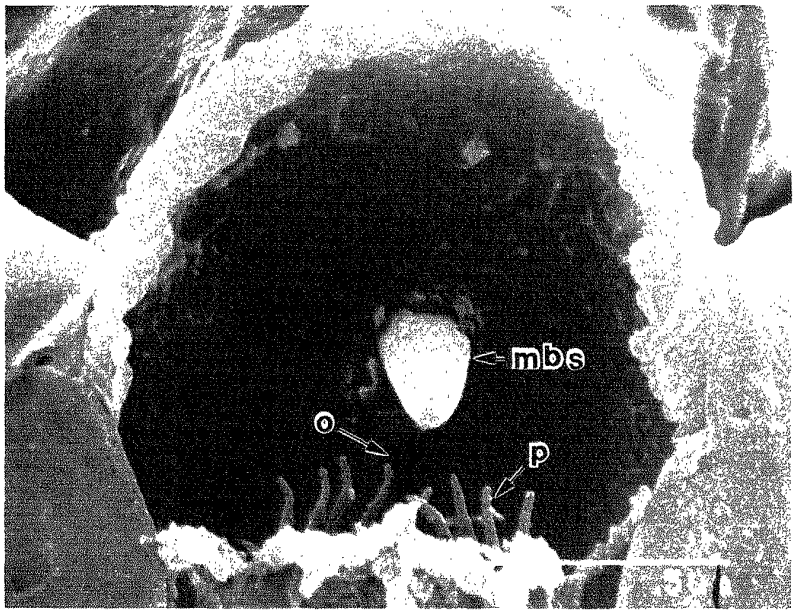

Figure 7. SEM of labral pad showing: (mbs) tip of mandibular stylet, (o) opening in pad for stylet protraction and (p) ventral papillae.

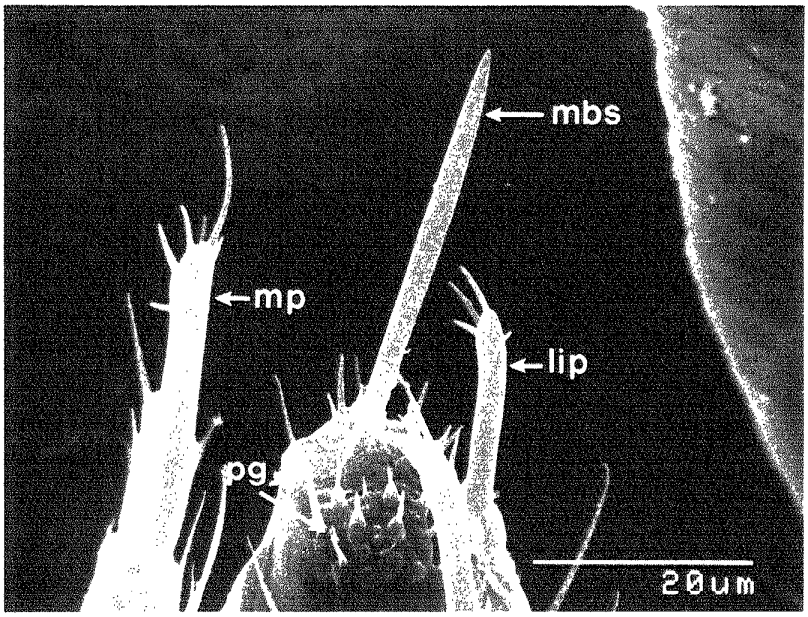

Figure 8. SEM of mouthcone showing: (mbs) protracted mandibular stylet, (lip) labial palp, (pg) paraglossa and (mp) maxillary palp.

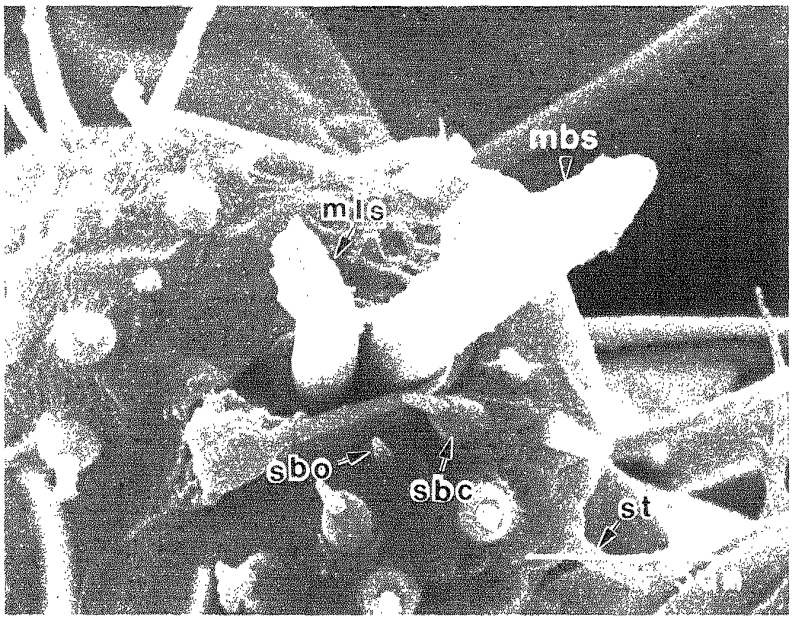

Figure 9. SEM of tip of mouthcone showing separating paraglossae: (mls) curved pair of maxillary stylets, (mbs) single mandibular stylet, (sbo) sensillum basiconicum without a distinct cuticular collar, (sbc) sensillum basiconicum with a distinct cuticular collar and (st) sensilla trichodeum.

The maxillary stylets are capable of being extended or withdrawn singly (Fig. 10) or together (Figs. 9, 11) and each is equipped with an internal longitudinal groove that, when the two stylets are interlocked, provides a hollow tube for withdrawing food material from the underlying cells (Mound 1971). Adults of *F. bispinosa* have a subterminal opening (so) on the maxillary stylets (Fig. 10) and their tips are asymmetrical (Figs. 10, 11). The right stylet tip is larger and slightly broader than that of the left. Maximum observed protraction of the maxillary stylets was 50 μm for one *F. bispinosa* specimen that had been exposed to chloroform while feeding. This length corresponds to the average depth of feeding injury observed in citrus flowers and developing buds (C.C.C. & D.S.A., unpublished data).

A light micrograph of the somewhat flattened mouthcone of a *F. bispinosa* female is shown in Figure 12. The labral pad (lp) and ring (lr) were distorted and pulled out of position in this preparation allowing a clearer view of several otherwise overlapping structures. The hypopharynx (h) is exposed as well as the food canal (fc) in its anterior surface and (e) indicates the tips of the two maxillary stipites (Fig. 12). The sclerite of the labial glossae including associated sensilla is indicated by (slg).

Cross sections were prepared for TEM and provide a clearer view of the arrangement of the principal internal structures of the mouthcone to illustrate their position and relative size (Figs. 13-15). Figure 13 shows a cross section of the mouthcone around 10 μm above its apex. The outer two elements are the labial paraglossae (pg). Anteriorly, the fused glossae (fg) are surrounded by the labral pad (lp). The labrum (lm) is located in the center and encloses the two irregular, broadened tips of the maxillary stylets (mls) and three parts of the irregular tip of the hypopharynx (h) in this section. The mandibular stylet (mbs) contains three diverging sensory dendrites (d). At this level, the food and salivary canals are not present.

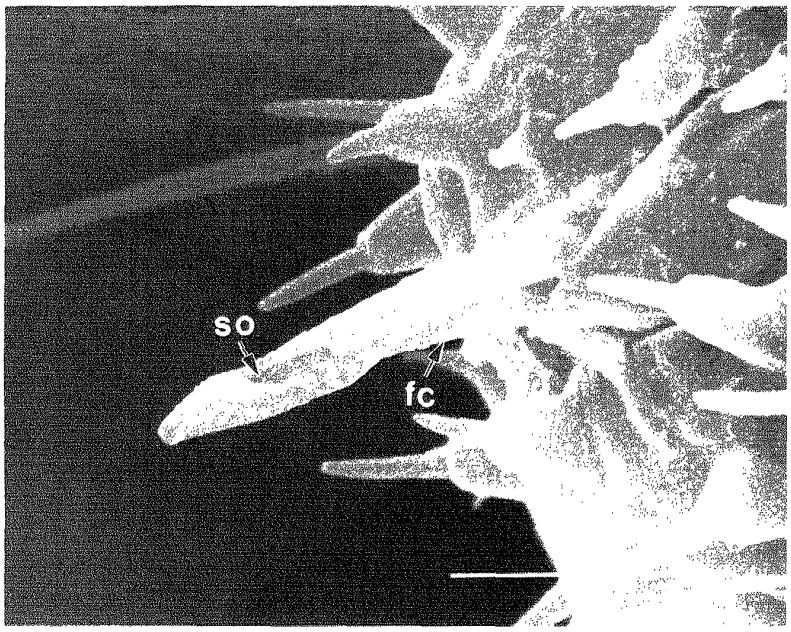

Figure 10. SEM of tip of mouthcone, showing the irregular shape and (so) subapical opening of the right maxillary stylet with its grooved interior (fc) forming half of the food channel.

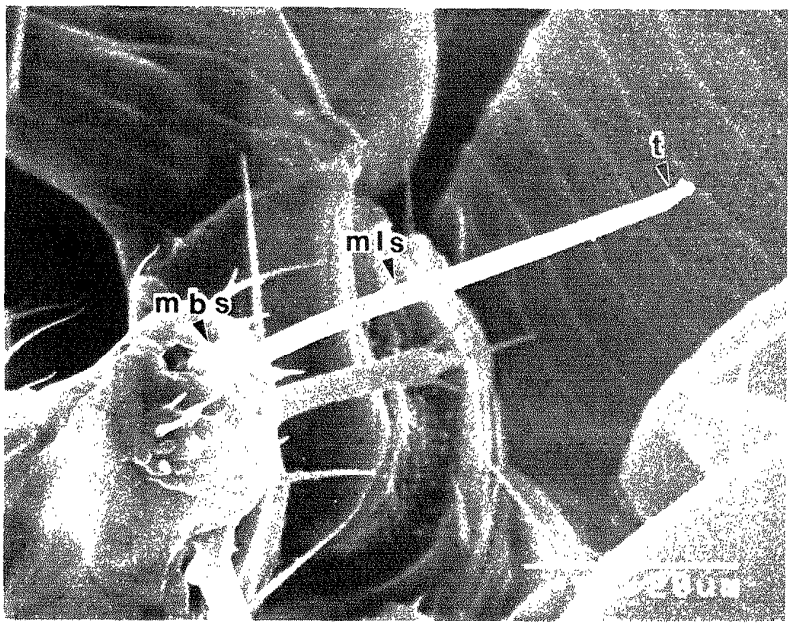

Figure 11. SEM of tip of mouthcone showing: (mbs) tip of mandibular stylet, (mls) paired maxillary stylets and (t) irregular-shaped tip of stylets.

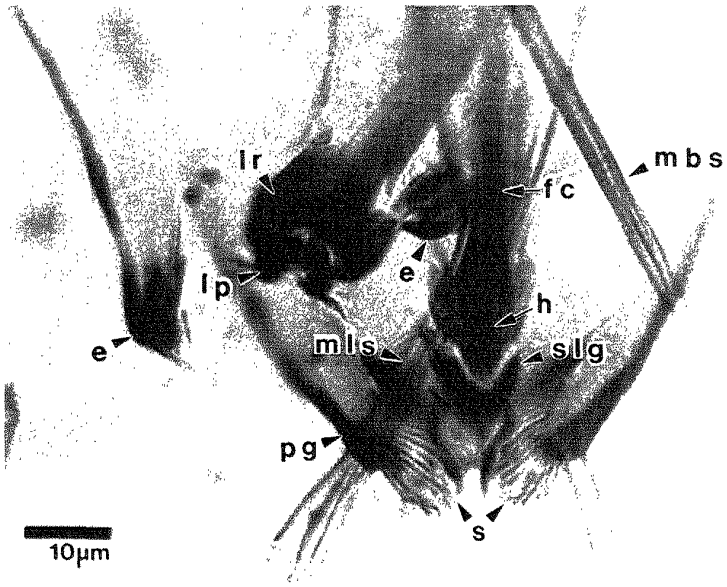

Figure 12. Light micrograph of whole mount preparation of the mouthcone of *F. bispinosa* showing: (lr) labral ring, (lp) labral pad, (slg) sclerite of labial glossa, (s) sensilla of labial paraglossae, (e) tips of maxillary stipites, (fc) food canal in anterior wall of hypopharynx (= precibarium), (h) hypopharynx, (mbs) mandibular stylet, (mls) maxillary laciniae and (pg) base of paraglossa.

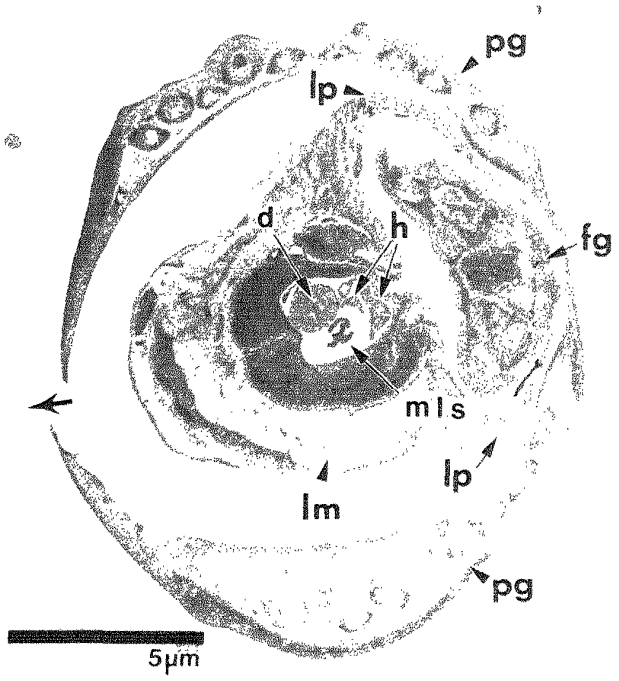

Figure 13. Transmission electron micrograph (TEM) showing cross section of the mouthcone of *F. bispinosa* about 10 μm from the tip with: (pg) labial paraglossae (lm) labrum, (fg) fused glossae, (lp) labral pad, (d) mandibular stylet with three sensory dendrites, (mls) tips of maxillary stylets and (h) hypopharynx. Large arrow points to front of insect.

The next cross section (Fig. 14) is around 40 μm proximal to the tip of the mouthcone and clearly shows the presence of both food and salivary canals. The labrum (lm) is situated anteriorly (Fig. 14) with the two maxillary stipites (ms) on either side and the prementum behind (pm). The hypopharynx (h) is located in the center with the food canal (=precibarium) (fc) in its anterior wall and the salivary canal (sc) in its posterior wall. Located on either side of the hypopharynx are the two maxillary stylets (mls). The larger, single mandibular stylet (mbs) is located anterior to the left maxillary stylet. It is supported by grooves in the hypopharynx and in the inner, membranous wall of the left maxillary stipes (Fig. 14). A similar arrangement occurs in larvae of *H. verbasci* (Heming 1978). Both maxillary stylets have recessed areas in the inner walls of the adjacent stipites that appear to also provide a degree of support. Closer examination of the stylets reveals the presence of four sensory dendrites in each lacinia and a central bundle of three dendrites (d) in the mandibular stylet (Fig. 15). The mandibular stylet of *H. verbasci* appeared to lack sensilla when viewed by SEM (Heming 1978). The mandible of *F. bispinosa* is solid with the exception of the small innervated channel and not hollow as previously reported for *L. cerealium* by Chisholm & Lewis (1984) and for *S. citri* by Wiesenborn & Morse (1989).

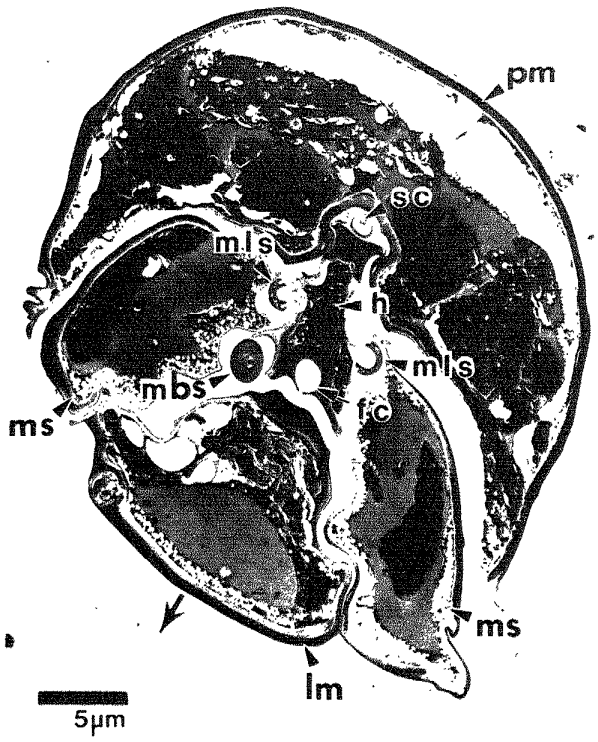

Figure 14. TEM of cross section of mouthcone of *F. bispinosa* taken about 40 μm from tip, showing: (lm) labrum, (ms) maxillary stipites, (pm) prementum, (h) hypopharynx, (mbs) mandible, (mls) maxillary laciniae, (fc) food canal and (sc) salivary canal. Large arrow points to front of insect.

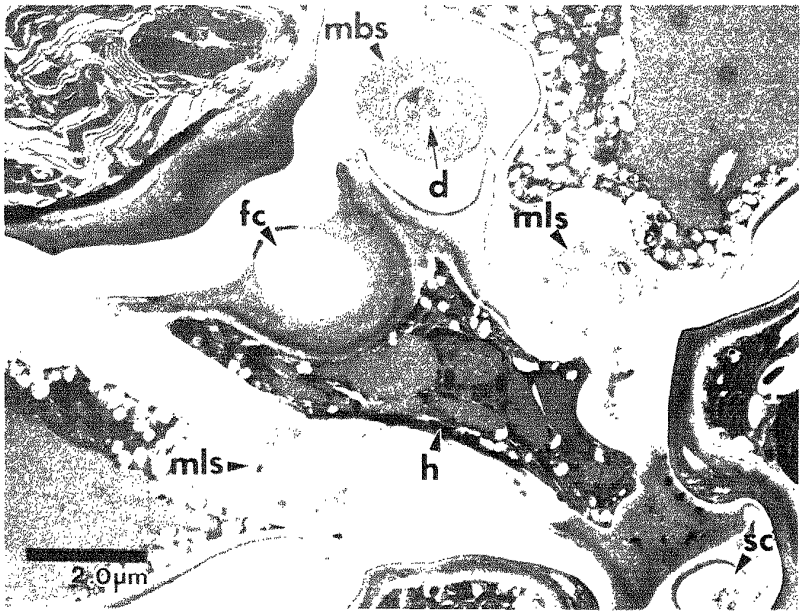

Figure 15. Enlargement of previous TEM showing: (mbs) mandible with (d) three sensory dendrites, (mls) maxillary laciniae with associated dendrites, (fc) food canal, (h) hypopharynx and (sc) salivary canal.

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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.

POTENTIAL CAUSES OF THE PEAR THRIPS OUTBREAK IN SUGAR MAPLE

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Introduction

No one knows what caused the 1988 outbreak of pear thrips, *Taeniothrips inconsequens* (Uzel), in sugar maple, *Acer saccharum* Marsh., in the northeastern United States. As an entomologist and ecologist who knows even less about this insect than most of the authors of this volume, I cannot presume to understand the causes of this event any better than anyone else does. This essay will of necessity be highly speculative.

Nonetheless, I will outline the kinds of things that must have happened to generate such an outbreak by this insect. There are really two issues involved in this particular case. This pest is called the "pear thrips" because it feeds primarily on plants in the Rosaceae, mainly in orchards (Parker et al. 1988). So the first question we might ask is "How has this insect come to feed on plants in quite unrelated families?" The second question that arises is the same one asked about every pest, namely, "Why are there so many of them?" After all, a pest is a species that is too abundant in a place where it is unwanted.

I will begin by reviewing current ideas about how insect species may add new host species to their diets. Then I will examine some common general hypotheses concerning causes of pest outbreaks and attempt to relate them to the pear thrips situation.

Colonization of Sugar Maple

The literature suggests that maple may be a relatively new host for the pear thrips (Cameron et al. 1916, Simons 1985, Stannard 1968). It is very difficult to be certain about such an assertion. Information in the pest management literature suggests that pear thrips feeds heavily on 15 or more forest tree species, but quantitative data are lacking (Lewis 1973, Simons 1985). We will have to assume for the moment that the favored and probably the original hosts for this insect were orchard trees in the Rosaceae (Borror et al. 1981). That makes it a bit surprising that beginning around 1979 pear thrips was observed doing quite well on maples in northeastern Pennsylvania (Simons 1985).

Pear thrips appears to have acquired the ability to complete its life cycle on sugar maple, which means the insect has acquired the ability to recognize, oviposit, feed, develop and reproduce successfully on the plant. The probability of combining all of the traits necessary for success at each step, as well as accumulating the correct combination of genes for this, should be quite low. Even if the female recognizes and oviposits on the plant, the offspring have to be able to recognize that plant to accept it and begin feeding. Feeding stages must have the right physiological traits, including biochemical adaptions for digestion, detoxification and development on that food. Solving the "chicken and egg" problem of how phytophagous insects integrate behavioral recognition with physiological adaptation when they colonize new hosts continues to elude theoreticians and field biologists (Futuyma 1983).

The taxonomic, evolutionary, and likely chemical distance between sugar maple (Aceraceae) and rosaceous hosts exacerbates this problem in the case of pear thrips. Although there are exceptions, we generally expect the chemical features of closely-related plants to be more similar than those of distantly-related species. When these features influence acceptability and suitability of the plant to an insect species (e.g., allelochemicals), we expect any insect species to switch among closely-related hosts more easily. This scenario seems unlikely for the possibly recent addition of sugar maple to the pear thrips' diet.

Maples and rosaceous trees do produce some of the same broad classes of allelochemicals. Both families produce a range of phenolic compounds, and members of each may produce alkaloids (Gibbs 1974, Barbosa & Krischik 1987). However, the alkaloidal structures differ substantially between the two families, and we know little about the phenolics of either. Members of the Aceraceae produce a fairly novel class of tannins ("acertannins") not found elsewhere (Bate-Smith 1977). Apples (genus *Malus*) produce a nearly unique set of monomeric phenolics (e.g., phlorizin) and other rosaceous trees produce species specific flavonoidal compounds (Robinson 1980). Rosaceous tree species, but not maples, commonly also produce cyanogenic glycosides (Robinson 1980, Gibbs 1974). These observations suggest that there may be substantial biochemical barriers to exploitation of maple by rosaceous-adapted thrips.

Allelochemicals do not present the only barriers to host plant use. Many biological and physical factors interact to determine the likelihood that an insect species may "colonize," or develop the ability to complete development on, a new host plant species. Janzen (1968) suggested an "archipelago model" of adaptation to host plants, in which the degree of similarity between any two plant species in a variety of traits influencing insect success indicates the "ease" with which the two plants may be incorporated into the same insect's diet over ecological or evolutionary time. Factors of importance include refuge from physical factors, susceptibility to natural enemies, seasonal and spatial availability of suitable tissues, and physical traits of the plant (e.g., leaf surfaces). In this model, plant species are visualized as "islands," the distances among which are defined by similarities and differences in features influencing insect use. Similarity in one or more features may reduce barriers to colonization, but could be balanced by differences in others. Unfortunately, we cannot yet rank the importance of these various influences in any useful way (Bernays & Graham 1988, Smith et al. this proceedings).

Of course, the host's environment can also influence the likelihood that an insect will survive to oviposit again on the same host. Habitat parameters, both climatic and edaphic, may determine this

barrier independently of host plant traits as food. In the case of pear thrips, low overwintering success in soil or litter could reduce the likelihood of adapting to host species growing in marginal habitats. Use of either or both hosts would then depend on the presence of tolerable or favorable physical conditions (e.g., soils, litter depth and moisture, etc.) in stands of both hosts.

Herbivore susceptibility to natural enemies (parasites, predators and pathogens) often differs dramatically among hosts (Brower 1958). An insect species' ability to exploit a new plant species could be blocked by increased risks there, but it could also be facilitated by increased "risk-free space" (Brower 1958, Bernays & Graham 1988). In the case of maple and orchard trees, we have no information to help infer a conclusion about this effect, and the impact of enemies on pear thrips appears to be unknown, even in orchards. One could imagine that pear thrips might escape an enemy important in orchards by colonizing maple, but of course this would require overcoming other barriers to the use of maple.

The product of the probabilities of overcoming all of these barriers must be rather small. Obviously, the pear thrips has overcome what might be significant barriers to become successful on sugar maple. What factors may have facilitated this?

Frequent encounters with a new host species probably facilitate dietary expansion or switching (Futuyma 1983). Although originally far more abundant in the western United States than in the East, the pear thrips has no doubt been present in eastern orchards for some time. The large number of orchards within the distribution of sugar maple must have provided ample contact with maple and plenty of opportunities for colonization. Futuyma (1983) has pointed out that the more frequent such encounters become, the more likely it is that individuals possessing traits necessary for success on the new plant will remain there to reproduce. Indeed, repeated colonization attempts and failure on the new plant ought to comprise strong selection favoring any adaptations to the new host that may arise. The spread of pear thrips through orchards in contact with maple may have provided these

opportunities, especially if gravid females are often blown out of orchards into surrounding maple stands. Expanding orchards would have a similar effect.

Cultural procedures may also play a role (Scriber & Hainze 1987). One might speculate that the ability to deal with maple chemistry could evolve as a form of cross resistance arising from selection exerted by pesticide use in orchards. The inverse situation, in which cross resistance to pesticides is induced as a function of feeding on different apple cultivars, has been observed in other pest insects (Yu 1986). Although we don't know enough about the biochemical basis of plant exploitation by thrips to draw serious conclusions, it is possible that the expanded development of new cultivars, or changing pesticide use, may have selected for thrips genotypes capable of exploiting new host species.

Dramatic changes in forest composition also have occurred since apple orchards became common in the eastern United States. More than half of the observed forest pest outbreaks in the Northeast occurred after the major logging events and changes in forest structure that occurred from 1860 to 1900 (Nothnagle & Schultz 1987). We don't know that there is a functional relationship here. However, between 1860 and 1900 many trees were damaged during removal of other trees, and the forest structure changed. Among other things, forest succession was pushed back to earlier seres, of which sugar maple would be a minor component. The New England forests are now returning to the older, climax forest type as agricultural land use decreases. Perhaps the increasing dominance of sugar maple in recent years has increased contact with orchard insects like the pear thrips. Alternatively, the physical environment may also have been changed in such a way as to make various tree species susceptible to pests.

One feature of the pear thrips that could facilitate host switching and the development of high population densities is its parthenogenic mode of reproduction. Bush (1974) proposed a model of host race formation by herbivores in which he pointed out that switching is facilitated if mating by adults is linked to the host. This link (e.g.,

mating on or near the oviposition site) ensures that male and female genotypes containing mutations permitting exploitation of a new host are combined in offspring feeding on the new host. This would increase the representation, and hence population size, of "preadapted" genotypes among offspring starting out life in a new environment (host), and should increase the likelihood that a new population capable of exploiting the new host becomes established.

Parthenogenesis in the pear thrips may provide an alternative means of increasing the genetic similarity among sibs produced by a single mother colonizing a new plant. Since that mother must recognize the new host to oviposit there, she places her genetically-similar offspring, which are likely to share most of her genes, together on the new host. If the mother's ability to recognize and oviposit on the new host (sugar maple) has a genetic basis, it is likely that most, if not all, of her offspring will carry the same trait. This would establish an entire population of "preadapted" thrips almost instantaneously, compared to outcrossing insect species in which many of the sibs may not carry the host-recognition genes of the maternal parent. Because parthenogenic species can establish larger populations of potentially adapted individuals when colonizing a new host, I suggest that adaptation barriers may be overcome by them more quickly than by sexually reproducing species. This may help explain what appears to be a sudden, explosive appearance of pear thrips on sugar maple.

It is impossible to determine the course of host-switching by an insect herbivore without knowing the details of plant traits and insect feeding, behavior, life history and habitat requirements. It is also important to put this information in a phylogenetic context, with comparative studies of related species. Research has not been extensive or intensive enough to provide a good basis for conclusions about pear thrips on sugar maple. However, given that the switch has occurred, what factors may influence the success of pear thrips on sugar maple trees and result in apparent "outbreak?"

Possible Outbreak Causes

There are almost as many hypotheses about the causes of pest outbreaks as there are investigators (Barbosa & Schultz 1987). I can focus here on only a few very popular ones. We need to beware of the use of the word "causes," because truly mechanistic studies are rare. The literature on pest outbreaks is instead dominated by correlative studies that generally serve to refine hypotheses rather than test or refute them.

For example, climate and weather variables are often identified as triggers, cues or actual causes of pest outbreaks in a particular forest system (Martinat 1987). The hypothesis that drought stress is a cause of pest outbreaks in forests is as old as outbreaks themselves (Mattson & Haack 1987). In the particular case of the pear thrips, there is some evidence that populations increase in orchards during drought years. There are, however, no studies of mechanisms that may be involved. We might speculate that superior overwintering success could be involved, or that reproduction improves. The possibility that stress may make hosts either nutritionally superior or more poorly defended chemically is popular at present (Mattson & Haack 1987). Interestingly, however, the plant physiology literature tells us that almost anything can happen to tissue quality under drought stresses, particularly in woody plants. That is, there are published examples of plant species that become better or worse nutritionally, and that increase or decrease putative defenses under presumably stressful conditions.

In the case of the pear thrips, there are virtually no studies on what characteristics of the host plant make it better or worse as food for the insect. Low rainfall in the years during or prior to the recent observation of thrips on Vermont maples may or may not have influenced tree quality. Depending on tree species, presumptive defense compounds may increase or decrease under drought stress (Gershenzon 1984). In some species protein or amino acid contents

may change, altering food quality. Any guesses about what host stress will do in sugar maple to make the plant better or worse for pear thrips comprise sheer speculation at this point.

Climatic events can also shift plant phenology, including leaf chemistry and nutritional value. Because species like sugar maple undergo dramatic seasonal changes in leaf traits (Schultz et al. 1982), there may be periods of time during which sugar maple leaves resemble leaves of other species chemically, perhaps including orchard species. For example, the distinctive acertannins in maples do not develop higher concentrations until mid- to late-summer; early in the season, the phenolic chemistry of maples tends to be dominated by monomeric phenolics that may be more similar to those of rosaceous trees (Schultz et al. 1982). If maple (or orchard tree) phenology were shifted by climatic events for one or two seasons, this could open a "window of opportunity" for colonization and growth success by thrips. This in turn would facilitate both colonization of maple and population growth and might produce an outbreak.

Climate could also have impacts on pest insects independent of the host (Mattson & Haack 1987, Martinat 1987). However, such host-independent effects ought to occur in orchards as well as in maple stands. There is no evidence that pear thrips populations are increasing in orchards concurrent with the present sugar maple infestation, although the heavy use of pesticides in orchards could obscure effects of natural enemies or other factors.

Once thrips is feeding successfully on maple, its populations could escape regulation by various factors important in orchards. In this case, we would say it has entered what some evolutionary ecologists call a new "adaptive zone" (Ehrlich & Raven 1965), or at least a way of life in which the insect experiences few barriers to population growth. Natural enemies and pesticides comprise common barriers in the orchard setting, and these may be absent on maple. Ordinarily, in natural systems it is not clear that the failure of natural enemies leads to pest outbreak, even if the pest population appears to be regulated by enemies at low density (Southwood & Comins 1976).

However, if pear thrips escapes an effective regulatory agent while living on maple (and if maple is suitable food), then its populations may achieve higher densities than are usually seen in orchards. Considering the degree to which insect populations in orchards are usually suppressed by pesticides, colonization of maple could produce an "outbreak" merely by eliminating that factor. If sugar maple were truly superior food, then rapidly growing pear thrips populations could even escape the regulatory impact of an enemy that followed it there. Information about the influence of food quality on thrips reproduction and about natural enemies is far too inadequate to propose more specific hypotheses.

In this light, it is important to consider the possibility that the pear thrips populations we observe in sugar maple stands do not comprise an "outbreak", i.e., they do not represent "unusually" high densities. Present thrips densities on maple may represent the overall carrying capacity of maple for this insect. We may continue to observe unabated high densities for the foreseeable future, now that the insect has managed to colonize this species.

Recent theory suggests that insects whose intrinsic rate of natural increase and certain other attributes conforms to certain theoretical criteria may be destined to exhibit irruptive population dynamics. It is difficult to demonstrate statistically that any pest outbreak is periodic, i.e., that it has a demonstrable cycle of "*N*" years. Hence, mechanisms that yield outbreak need not produce regular periods in outbreak cycles. May (1985) has suggested that pest species represent an adaptive type, or a particular way of life in which high reproductive rates and other traits combine to yield outbreak dynamics in chaotic fashion. In either case, density-dependent regulatory factors are usually operating, at least during the crash of epidemics. Anderson & May (1980) point out that use of artificial controls (e.g., pesticides) in such cases may be self defeating, in part because density-dependent regulation (e.g., via disease) is thwarted.

In attempting to control pear thrips on the sugar maple, we need to keep in mind the possibility that the commonly applied pesticides may fail on the new host plant. In particular, biological pesticides may fail because of the chemistry of the host (Schultz & Keating in press). Integrated pest management should account for the specific interactions among the plant, insect, and insect's enemies.

It is abundantly clear that no control program can succeed until we understand what the pear thrips eats, what food quality factors are important to its success, what role natural enemies play, and the importance of physical factors. Our information on all of this is woefully inadequate; we barely understand the basic biology of this insect. We must be prepared to assemble a major research effort (with significant support), and to spend significant time studying the basics of this system if we hope to design effective and environmentally sound control efforts.

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Discussion Period

Question: We're used to thinking of host plant chemistry attributing to outbreaks, are you suggesting that under some circumstances the host plant actually welcomes some new pests, and that the attributes of the host plant somehow contribute to the accumulation of pests?

Schultz: I think that almost all sugar maple trees very likely pass through windows of opportunity for colonization, ecologically and perhaps in terms of age. Apparently certain aged trees are more susceptible to this insect than others. My guess would be that this insect wouldn't be able to cross over as easily if maple didn't pass through a phase either each year or during its life time that made it much more like a pear than it is otherwise. I suspect there has been selection pressures on this insect for the ability to deal with the tree. It probably has a window of opportunity, though it appears to be doing well on both sides of the window as well. In 1909 Moulton hypothesized that the reason pear thrips were so successful on pears is that it has clustered flowers. Maples also have clustered flowers. In fact, there must be 150 species of trees in northeastern North America that have clustered flowers. Therefore the flower type alone must not be the characteristic that distinguishes maples from other potential thrips hosts.

I tend to focus on leaf feeding because that is my specialty. I think the suggestion that availability in spacial distribution of a resource like the flowers is interesting but there are other maples that have similar flower clusters and I'd be curious to know if the insect is successful on those. However, maples differ greatly in their secondary chemistry which may also influence host susceptibility. This must be integrated with other host information.

Question: Do you assume that there is genetic variability between the pear thrips on pears and those on maples?

Schultz: Certainly that is possible, but I have no idea. There are many potential sources of genetic variation. The statement that all of the genetic offspring of a female are identical to her is not strictly speaking true. Considering the number of generations of pear thrips in North America, I am sure we are now looking at other genotypes. I don't assume that the maple feeders are a different genotype but they probably are. If not, there is a tremendous congruency of characteristics between maple and pear.

What makes this question so interesting to me is I can't figure out how an insect that is a good Rosaceae feeder switches over to a different host so successfully. For other insects that feed on a wide variety of plants, when a new plant is introduced into the system, the insect may just include it in the host range and there is no fundamental difference in population structure. That could apply here.

David Jenson pointed out that leaf eating insects eat leaves and that is determined by the unique characteristics of the leaves and all the other ecological circumstances that may be available. Until we know what the requirements are for thrips success we can in no way indicate what plants should and should not be hosts. It is just astonishing to me that we have no idea how this insect makes its living. I assume that nitrogen is important to it, and secondary chemicals can influence it as well.

Comment: I want to mention a few points about the genetics of thrips. Thrips have what we call myotic parthenogenesis, whereby the polar body fuses with the opening so you actually get very little genetic variation. It is possible however that pear thrips males do occur in the United States. They might be so short-lived that they have not been found. I worked on a species of thrips in Colorado that only occurs for a very short time and in very localized populations each season.

In some species of thrips the males are not very important to female reproduction and there are other species in which the males are present and needed for reproduction.

Question: Are there any comprehensive genetic studies that really identify the system of inheritance in thrips?

Answer: No.

Question: Has anyone investigated the correlation between the outbreak of this pest and the stress on sugar maple trees caused by acid rain?

Schultz: I'm not aware of anyone doing such work associated with acid rain and the pear thrips outbreak. I haven't seen any evidence that there is a significant relationship between any major insect outbreak and acid rain, and quite frankly I wouldn't expect there to be much of one. I see the contribution of acid precipitation to the leaf as minor.

A possible factor contributing to this outbreak might be drought. A one-to-three year drought could have a profound effect on the physiological state of sugar maple trees and make them unusually susceptible to thrips. I do not know however why maple might be susceptible and beeches and birches are not. One report I found in the literature pointed out that pear thrips is particularly successful and prone to outbreaks in orchards during drought years, presumably as a result of higher winter survival.

The effect of tree phenology on thrips success and damage remains an important question. We watch the buds burst and the leaves get bigger, but many things are going on inside the leaf at different rates that we don't see. Chemicals are coming and going. In oak trees the composition of the molecules in the young leaves changes daily over the first 10 days of leaf expansion. If one of those compounds is essential to one of these insects, the synchrony of the insect and tree becomes critical. Because we do not yet know what is crucial to the survival of pear thrips, it is impossible to know what characteristics of maple phenology are important? One of the crude changes that occurs during leaf development is that the leaves get tougher day by day. I think the issue of phenology is critical. Maples may go through a stage in which they are not like other Rosaceae trees.

The question remains why pear thrips haven't been a pest problem for the past 20 years. I'm really curious about that. We've had apples, pears, and sugar maples in the Northeast for a long time and the insect has been in the Northeast since the turn of the century. So I don't know why all of a sudden it has managed to find sugar maples suitable. These facts suggest to me that a significant shift has occurred in the thrips ability to deal with this host. Perhaps the trees have changed since the thrips arrived, possibly due to some predisposing factor associated with this outbreak.