Ecology of Thrips

Joe Funderburk

Professor of Entomology, University of Florida. North Florida Research and Education Center, 155 Research Road, Quincy, Florida 32351 USA.

E-mail: jefunderburk@mail.ifas.ufl.edu

Summary: The Thysanoptera are opportunistic species exploiting intermittently occurring environments. The life history strategy is preadapted from the detriophagous ancestral group, and the need to succeed in a habitat in which optimal conditions are brief. The most advanced species are the flower thrips, primarily species of *Frankliniella* and *Thrips.* Most thrips are r-selected with population attributes that were believed to result in thrips outstripping the capacity of natural enemies to regulate populations. Recent research has revealed that species of *Orius* (Heteroptera: Anthocoridae) and *Thripinema* (Tylenchida: Allantonematidae) are important natural enemies of flower thrips that suppress populations and cause local extinctions. Elucidation of multitrophic interactions that affect abundance and persistence of populations of prey and natural enemies in field crops is resulting in improved, ecologically based management programs for thrips and tospoviruses. Although many of the highly vagile species of thrips exhibit mass flights and are found in remote regions, there is little quantifiable information of local movements, dispersal rates, and patterns of migration. Better understandings of population turnover, local extinctions, and colonization of thrips vectors of tospoviruses are needed to effectively manage these emerging threats to global agriculture.

This paper follows my oral presentation at the meeting in Reggio Calabria, Italy. Information sources are added and certain points are elaborated. The text is an overview of issues in the ecology of thrips. Other papers in this volume from talks in the ecology session and the thrips and plants session provide more elaborate detail. Plants, thrips, and tospoviruses are considered as an integrative system in keeping with the theme of the meeting, and I have found the addition of sub-headings in this paper impractical.

Conventional wisdom is that, although it is easy to obtain large numbers of thrips, their small size and claustral habits make it difficult to investigate directly the reasons for changes in population size. Even though the order Thysanoptera contains a large number of species many of which are very common (Moritz et al. 2001), the many factors affecting thrips numbers are not understood. When the book *Thrips As Crop Pests* edited by Trevor Lewis was published in 1997, there were no clear examples showing that natural enemies were able to suppress populations of thrips. Kirk (1997) speculated in his chapter that the difficulties associated with the study of thrips may account for the lack of good quantifiable information about the role of natural enemies.

Other authors including Loomans et al. (1997), Butt and Brownbridge (1997), Parrella and Lewis (1997), and Parker and Skinner (1997) concluded that natural enemies must not be important.

Mound (1997) speculated that the population attributes of thrips outstripped the capacities of natural enemies to suppress populations. The life history strategy presumably is preadapted from the detriophagous ancestral group, and the need to succeed in a habitat in which optimal conditions are brief. Species of thrips generally are *r*-selected with population characteristics that include vagility, a short generation time, a moderately broad food tolerance, a tendency towards parthenogenesis, and possibly a competitive breeding structure that promotes aggregation. Agricultural crops provide new opportunities for quick colonization and establishment of large populations of opportunistic thrips, and some species are important pests.

The most advanced species are the flower thrips, primarily species of *Thrips* and *Frankliniella*. Pollen provides nutrients for greater egg production (Tsai et al. 1996), and the adults of most species feed in the flowers of a wide range of the available plant species, including those that are not suitable reproductive hosts (Chellemi et al.

1994). Young leaves are exploited by adults when flowers are scarce (Teulon et al. 1993, Toapanta et al. 1996). The leaves are preferred as a more stable source of food for developing larvae in some species (Funderburk et al. 2002). The common flower thrips in northern Florida are three native species, including *Frankliniella bispinosa*, *Frankliniella tritici*, and *Frankliniella fusca*, and a non-native species *Frankliniella occidentalis*.

Fifty years ago, Davidson and Andrewartha (1948a, b) published data on the number of *Thrips imaginis* in rose flowers collected for fourteen years in Adelaide, Australia. They observed no natural enemies of importance, and Andrewartha and Birch (1954) concluded that population size was determined by the weather with no room in a multiple regression analysis for density-dependent factors to be important. This data of thrips collected from roses in a garden hedge formed the main basis for their general rejection of density-dependence in regulation of animal populations. They argued that the "dogma" of density dependence ignored the fluctuations in the actual rate of increase with time, which may be induced by seasonal and other fluctuations with the components of the environment, and it also ignored the heterogeneity of the places where animals live.

A controversy erupted with other ecologists arguing that the Andrewartha and Birch (1954) model merely showed relationships between weather parameters and population estimates. Smith (1961) showed that their multiple regression model was not appropriate for the conclusions they reached. He argued that predation, parasitism, and other density-dependent mortalities not identified in the Davidson and Ardrewartha (1948a, b) studies likely interacted with the capacity of the thrips to increase, which would be a function of flower density, so as to produce a variable equilibrium level. Only in September and October, when a marked increase in flowers occurred, did the variance of the population behave according to the requirements of a density-independent system. Many authors including Varley et al. (1973) and Mound (1997) concluded that the roses were not a reproductive host and that the data merely reflected population fluctuations on the surrounding reproductive plant hosts. Boissot

et al. (1998) found that declines in population abundance of *F. occidentalis* were not related to unfavorable temperatures or other environmental factors and that an increase in abundance of a native *Orius* sp. may have been responsible.

Although the highly vagile nature of thrips and their other population attributes suggested an ability to outstrip regulatory capacities of natural enemies (Mound and Teulon 1995, Mound 1997), Funderburk et al. (2000) showed that populations of *Orius insidiosus* (Heteroptera: Anthocoridae) are effective predators of thrips in field peppers during the spring when thrips were rapidly colonizing and developing in flowers. Predation resulted in suppression of adults and larvae of *F. occidentalis*, *F. tritici*, and *F. bispinosa* once the predator:prey ratio reached about 1:200, and near extinction of thrips populations a few days after predator : prey ratios reached 1 to 40. The population dynamics of predator and prey in this field study were similar to the predictions based on ecological models of the intrinsic capacity of the predator to suppress thrips and to empirical data for coherent populations of predator and prey in greenhouse systems (Sabelis and van Rijn 1997).

The predator:prey ratio has proven a reliable predictor of the effects of *O. insidiosus* in suppressing populations of thrips under field conditions. Figure 1 shows the annual cycles of abundance of *F. occidentalis* and *O. insidiosus* in an alfalfa field in the Aconcagua Valley in Central Chile (R. Ripa, F. Rodriguez, J. Funderburk, and F. Espinosa, unpublished). Alfalfa is an excellent reproductive host for *F. occidentalis*, and weather conditions become very favorable for rapid population buildup in the spring. Numbers of adults peak in November or December. Numbers of thrips larvae peak two to four weeks later when numbers of *O. insidiosus* are sufficient to result in suppression of populations. Persistence of the predator during summer and fall prevents buildup of the nearly extinct populations of *F. occidentalis*. The Aconcagua Valley is about the same latitude in the Southern Hemisphere as Adelaide, Australia. The annual cycle of abundance of the adults of *F. occidentalis* in alfalfa in Chile (Figure 1) was similar to the annual cycle of abundance of the adults of *T. imaginis* in roses in Adelaide, Australia reported by Andrewartha and Birch
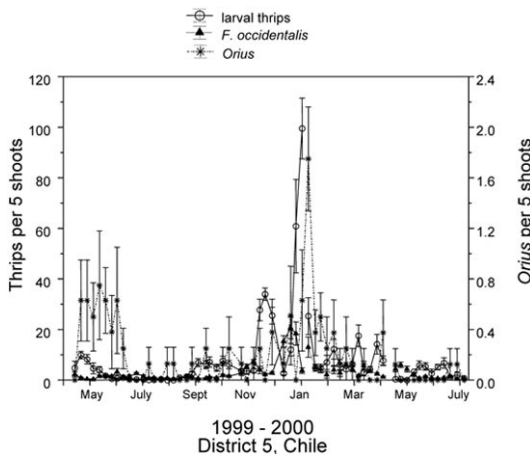
Fig. 1. Annual cycle of population abundance of Franklniella occidentalis and the predator Orius insidiosus in alfalfa in the Aconcagua Valley in Central Chile (unpublished data).
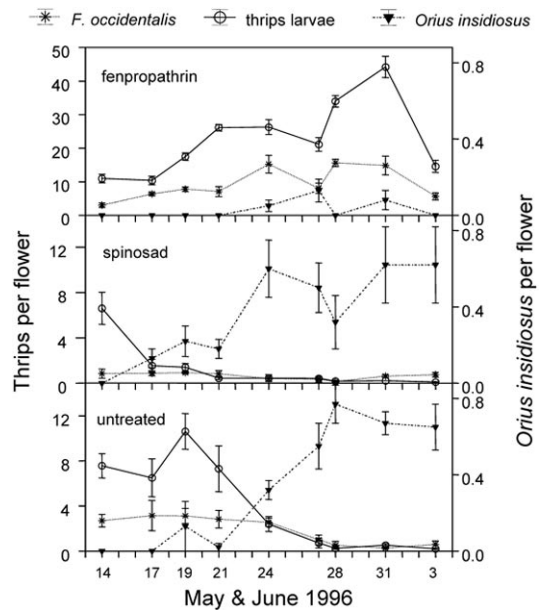

Fig. 2. Mean densities (+ SEM) of Frankliniella occidentalis and Orius insidiosus per flower in selected insecticide treatments applied to sweet pepper in north Florida adapted from Funderburk et al. 2000.

(1954). However, the roses are not a reproductive host for *T. imaginis* and Andrewartha and Birch reported that natural enemies were not observed.

Different tactics can be used to modify the densities of thrips and *O. insidiosus* in field pepper, thereby affecting population dynamics. Applying the insecticide spinosad reduces the number of the prey in relation to the predator, thereby resulting in more rapid extinction of thrips populations (Fig. 2). Conversely, exclusion of the predator with the insecticide fenpropathrin results in continued abundance of thrips, as the predator : prey ratio never is sufficient to suppress the prey population. The number of *Frankliniella* thrips in relation to *O. insidiosus* also is altered by the use of different types of plastic mulches (Fig. 3). UV reflective mulch affects the ability of immigrating adults of both the predator and the thrips prey to locate the plant host. Compared to pepper grown on the traditional black mulch, suppression of the thrips population is delayed.

Sabelis and van Rijn (1997) speculated that *O. insidiosus* must have a strong urge to disperse and reach new prey patches once the local population of thrips is suppressed, because the females need many thrips to meet the energy requirements of egg production. They further speculated that the tendency of the predator to

disperse in search of prey should lead to a high chance for the population of thrips to recover. But, populations of *O. insidiosus* persist in field pepper after the thrips populations are nearly extinct (Figure 4). Numbers of *O. insidiosus* in relation to prey are sufficient to prevent buildup of the thrips population, and recovery of the locally extinct populations of thrips does not occur (Ramachandran et al. 2001).

Predators persist locally when populations of prey are nearly extinct by feeding on extrafloral nectaries or pollen. Species including *O. insidiosus* are able to complete development and oviposit on a diet of pollen (Richards and Schmidt 1996). Many plant species also produce domatia, small hair tufts or pockets on the lower surface of leaves, which provides refuges for predatory arthropods (Agrawal and Karban 1997). Species of *Orius* are more abundant on domatia-bearing plants where the eggs and nymphs are found within the domatia.

Ecological models and greenhouse experiments are showing the benefits to plants when they provide pollen as an alternative food
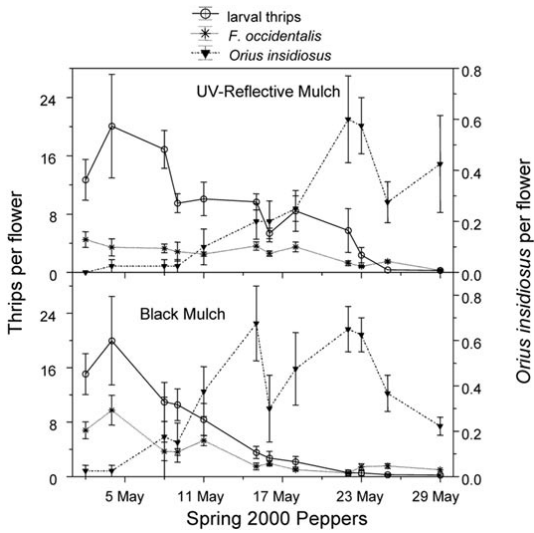
Fig. 3. Mean densities (+ SEM) of Frankliniella occidentalis and Orius insidiosus per flower in sweet pepper grown on a raised bed system of traditional black versus UV-reflective mulch in north Florida (unpublished data).
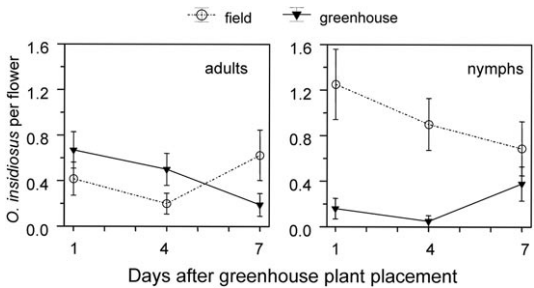

Fig. 4. Mean densities (+ SEM) of adult and nymphal Orius insidiosus per flower in untreated field and greenhouse plants on 1, 4, and 7 days after greenhouse plants were placed in the plots (data pooled over 5 weeks, n = 60 samples of 3-5 flowers) (adapted from Ramachandran et al. 2001).

Fig. 5. Mean number of Frankliniella occidentalis versus Frankliniella bispinosa predated per hour in Petri dishes with a single pepper flower.

for predators (Van Rijn et al. 2002). Populations of *F. occidentalis* settle at lower equilibrium values in the presence of pollen. Plants provide the extrafloral nectaries and pollen at specific sites. This allows the predators to aggregate and monopolize the food patches, resulting in a decrease of the numbers of *F. occidentalis*.

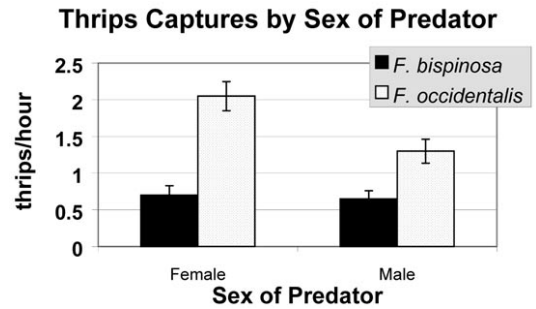The females of *O. insidiosus* need to move locally between pepper flowers in search of prey, because densities of prey in flowers usually are less than the predation rate of 12.5 thrips per day (Tommasini and Nicoli 1993). Ramachandran et al. (2001) studied local movement of predator and prey in field pepper. The adults of *O. insidiosus* moved rapidly between flowers in search of prey. Movement by *F. occidentalis* was limited, whereas *F. tritici* and *F. bispinosa* moved rapidly between the flowers. The males of each species moved more rapidly than the females. Rapid movement assisted *F. tritici* and *F. bispinosa* in avoiding predation, but *O. insidiosus* also moved rapidly. This attribute explains the predator's ability to suppress thrips even when populations are rapidly colonizing and reproducing in the flowers. Populations of each of these species decline greatly by late spring or early summer on crop and wild plant species in north Florida, but populations of *F. occidentalis* decline sooner than populations of *F. bispinosa* and *F. tritici* (Chellemi 1994, Funderburk et al. 2000, Ramachandran et al. 2001).

Behavior experiments confirm that rapid local movement assists thrips in avoiding predation. When single species of thrips are present, the predation rate of the females of *O. insidiosus* is about 1.5 prey per hour for *F. occidentalis* and *F. bispinosa*. (Waring, Funderburk, and Reitz, unpublished). However, *O. insidiosus* preys more effectively on *F. occidentalis* than on *F. bispinosa* when both species are present (Figure 5).

Another mechanism by which thrips can avoid predation is to utilize plant hosts unsuitable to the predator. The host range for *F. occidentalis* is especially broad, and it reproduces on many

plant species where it escapes predation from *Orius*. Tomato is an excellent example, but there is a tradeoff in that reproduction of *F. occidentalis* on tomato is very low (Brodbeck et al. 2001). The attribute of polyphagy may explain the species remarkable ability to establish and persist in ecosystems throughout the world (see Ripa et al. this volume). Interestingly, the persistence and abundance of *Frankliniella* species varies greatly among different regions of Florida. In north Florida, *F. occidentalis* can be found year-round and it is the most common species from winter to early spring when it is displaced by the increasingly abundant *F. tritici* and then *F. bispinosa* (see Reitz et al., this volume). Although *F. tritici* is extremely abundant throughout the central and eastern parts of the U. S., it does not persist in central and southern Florida where *F. bispinosa* is the only abundant species. The persistence and abundance of these *Frankliniella* species in Florida clearly is not related to the availability of plant hosts or to the suitability of the climate. Factors such as interspecific competition or differences in their ability to escape predation by *Orius* may be important.

Thrips use defensive behaviors against arthropod predators, including raising and lowering the abdomen, twitching the abdomen from side to side, or production of a droplet of anal fluid. The nymphs and adults of both sexes of *F. occidentalis* produce an anal droplet that mediates behavior of predator and prey (Teerling et al. 1993). The larvae move into refuges of webbing provided by *Tetranychus urticae* when *Orius* predators having fed on conspecific thrips threaten (Venzon et al. 2000).

Specialized parasites of thrips in the genus *Thripinema* are another important group of natural enemies. Described species occur in North America, Asia, and Europe (Tipping et al. 1998). An unidentified species of *Thripinema* infects *Thrips obscuratus* in New Zealand (Teulon et al. 1997). Another species that is morphologically indistinguishable from *Thripinema khrustalevi* infects *Frankliniella australis* in South America (Funderburk et al. 2003).

Nymphal and adult thrips are infected, and parasitism renders the females almost completely sterile (Loomans et al. 1997, Lim et al. 2001, Sims and Funderburk, unpublished). One heterosexual generation develops in the hemocoel of the adult thrips abdominal and thoracic cavities. The oviparous parasitic female releases eggs into the haemocoel and the motile vermiform larvae feed on the thrips' internal fluid. Mature larvae exit the host by boring through the wall of the midgut. From the midgut, the larvae move to the pyriform rectum where they reside for a period before issuing from the anus. It is not known when mating takes place. Free-living females attach to the legs of a thrips host after which it enters through the soft intersegmental membranes.

Local populations of *Frankliniella fusca* are suppressed to near extinction in peanut by parasitism from *Thripinema fuscum* when levels of parasitism reach 60 to 90 % during late spring or early summer (Funderburk et al. 2002; Funderburk, Stavisky, Momol, and Gorbet, unpublished). Short-term recovery of the population was observed during a period of very hot, dry weather, when the level of parasitism was reduced. Otherwise, populations remained extinct until harvest of the peanut crop. Numbers of *Frankliniella australis* adults and larvae in the flowers of *Cestrum parqui* in Chile are greatest
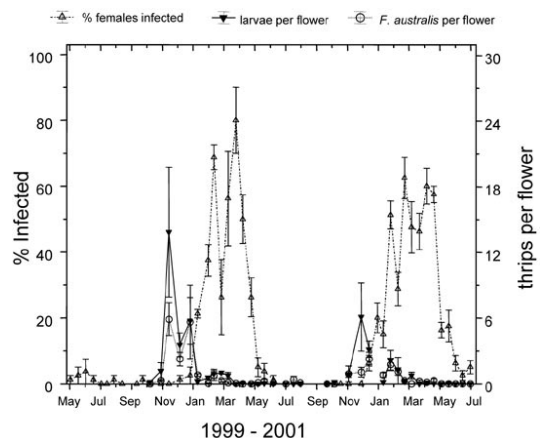

Fig. 6. Mean number (+ SEM) of adult and larval Frankliniella australis in the flowers of Cestrum parqui and mean percent parasitism (+ SEM) of the females, Aconcagua Valley, Central Chile (unpublished data).

in the winter and early spring when parasitism of the adult females is very low (Fig. 6). Populations decline in late spring and remain nearly extinct during summer and fall when parasitism is great. High levels of infection were reported for other species of *Thripinema* (Sharga 1932, Lysaght 1937, Reddy et al. 1982), which may indicate that natural suppression of thrips populations by species of *Thripinema* is widespread.

Groups of natural enemies other than *Orius* and *Thripinema* undoubtedly play an important role in the population dynamics of thrips. Overall, population turnover, colonization, and the spatial structure among local populations of thrips has received little detailed study. Thrips have been collected at great heights and far out over the oceans (Lewis 1997). Specific humidity conditions are required to prevent dessication of such wind-blown thrips, and the chance must be very rare that enough migrants survive to colonize fresh habitats. The occurrence of reproducing populations of highly vagile species in remote, isolated regions likely results from their ability to develop rapidly on a wide range of plant hosts. Mound (1997) reported, for example, finding *T. imaginis* in the flowers of *Acacia* and *Maireana* in the arid center of Australia, where the population is not able to persist year-round. This species apparently re-invades by breeding on species of semidesert plants that flower sporadically as conditions permit. Similarly, the adults of *F. australis* in Chile are found at mountain heights where flowering vegetation is scarce (L. A. Mound and J. E. Funderburk, personal observation). Conversely, populations of the less vagile *F. occidentalis* are restricted to the valleys. A plethora of studies purportedly studied movement by using variously colored sticky cards. These traps provide a measure of flight activity and population density, but the captures have yielded little understanding of local movements, emigration, immigration, and dispersal rates.

Many of the highly vagile species of thrips exhibit remarkable mass flights after developing in a density independent fashion on the abundant spring flowers (hence the lay names thunder flies, storm flies, and thunder bugs). Crops serve as islands for their aggregating populations. Vegetable crops in north Florida are beginning to flower in May when these mass flights occur (Salguero Navas et al., 1991, Chellemi et al. 1994, Funderburk et al. 2000). Ramachandran et al. (2001) studied local movement of the *Frankliniella* species in pepper in north Florida by placing plants that were raised in the greenhouse nearly free of thrips into the field plots. Puche and Funderburk (1995) used mark and recapture techniques to determine dispersal rates of *F. occidentalis* in the greenhouse. Marking and recapture of thrips using rhubidium chloride was very useful in determining local movements of *Frankliniella fusca* within a field of peanuts and also of estimating dispersal rates out of the peanut field (K. Ingram, J. Funderburk, and R. McSorley, unpublished data). Healthy males and females dispersed at a higher rate than those parasitized by *Thripinema fuscum*.

Many species of thrips have become established in new geographical areas. The most efficient vector of tomato spotted wilt virus, *F. occidentalis*, is nearly cosmopolitan. Single tactic approaches, such as insecticides for thrips control and resistant crop varieties for control of tomato spotted wilt, are not sustainable. An understanding of behavior and ecology of thrips is essential to the development of effective, sustainable approaches to the management of thrips and tospoviruses. Recent research has shown that two groups of natural enemies that occur worldwide are very important natural enemies of thrips. Undoubtedly, other natural enemies are capable of causing suppression and extinction of local populations. Understanding population dynamics of thrips and their natural enemies in the landscape should prove key to efficient and effective management of damaging populations of thrips and the spread both primary and secondary spread of tospoviruses.

References

Agrawal AA and Karban R. 1997. Domatia mediate plant-arthropod mutualism. *Nature* **387**, 562-563.

Andrewartha HG and Birch LC. 1954. *The distribution and abundance of animals*. University of Chicago Press, Chicago, IL.

Boissot NB Reynaud B. and Letourmy P. 1998. Temporal analysis of western flower thrips (Thysanoptera: Thripidae) population dynamics on Reunion Island. *Environmental Entomology* **27**, 1437-1443.

Brodbeck BV, Stavisky J, Funderburk JE, Andersen PC and Olson SM. 2001. Flower nitrogen status and populations of *Frankliniella occidentalis* feeding on *Lycopersicon esculentum*. *Entomologica Experimentalis et Applicata* **99**, 165-172.

Butt TM and Brownbridge M. 1997. Fungal pathogens of thrips. *Thrips as Crop Pests* (ed. Lewis T), pp. 399-434. CAB International, Wallingford, UK.

Chellemi DO, Funderburk JE and Hall DW. 1994. Seasonal abundance of flower inhabiting *Frankliniella* species (Thysanoptera: Thripidae) on wild plant hosts. *Environmental Entomology* **23**, 337-342.

Davidson J and Andrewartha HG. 1948a. Annual trends in a natural population of *Thrips imaginis* (Thysanoptera). *Journal of Animal Ecology* **17**, 193-199.

Davidson, J and Andrewartha HG. 1948b. The influence of rainfall, evaporation and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). *Journal of Animal Ecology* **17**, 200-222.

Funderburk JE, Stavisky J and Olson S. 2000. Predation of *Frankliniella occidentalis* (Pergande) in field peppers by *Orius insidiosus* (Say). *Environmental Entomology* **29**, 376-382.

Funderburk J. Stavisky J, Tipping C, Gorbet D, Momol T and Berger R. 2002. Infection of *Frankliniella fusca* (Thysanoptera: Thripidae) in peanut by the parasitic nematode *Thripinema fuscum* (Tylenchidae: Allantonematidae). *Environmental Entomology* **31**, in press.

Funderburk J, Ripa R, Espinosa F and Rodriguez F. 2003. Infection of *Frankliniella australis* (Thysanoptera) by the parasite *Thripinema khrustalevi* (Tylenchida: Allantonematidae) isolate Chile. *Florida Entomologist*, submitted.

Kirk WDJ. 1997. Distribution, abundance, and population dynamics. *Thrips as Crop Pests* (ed. Lewis T), pp. 217-258. CAB International, Wallingford, UK.

Lewis T. 1997. *Thrips as Crop Pests*. CAB International, Wallingford, UK.

Lewis T. 1997. Flight and dispersal. *Thrips as Crop Pests*.(ed. Lewis T), pp.175-196. CAB International, Wallingford, UK.

Lim UT, Van Driesche RG and Heinz KM. 2001. Biological attributes of the nematode, *Thripinema nicklewoodi*, a potential biological control agent of western flower thrips. *Biological Control* **22**, 300-306.

Loomans AJM, Murai T and Greene ID. 1997. Interactions with hymenopterous parasites and parasitic nematodes. *Thrips as Crop Pests* (ed. Lewis T), pp. 355-397. CAB International, Wallingford, UK.

Lysaght AM. 1937. An ecological study of thrips (*Aptinothrips rufus*) and its nematode parasite (*Anguillulina aptini*). *Journal of Animal Ecology* **6**, 169-192.

Moritz G, Morris DC and Mound LA. 2001. *ThripsID Pest thrips of the world*.CSIRO Publishing, Collingwood, Australia.

Mound LA and Teulon DAJ. 1995. Thysanoptera as phytophagous opportunists, *Thrips Biology and Management* (eds. Parker BL, Skinner M and Lewis T) pp. 3-19. Plenum Press, New York.

Mound LA. 1997. Biological diversity. *Thrips as Crop Pests* (ed. Lewis T), pp. 107-216. CAB International, Wallingford, UK.

Parker BL and Skinner M. 1997. Integrated pest management (IPM) in tree crops. *Thrips as Crop Pests* (ed. Lewis T), pp. 615-638. CAB International, Wallingford, UK.

Parrella MP and Lewis T. 1997. Integrated pest management (IPM) in field crops. *Thrips as Crop Pests* (ed. Lewis T), pp. 595-614. CAB International, Wallingford, UK.

Puche H and Funderburk J. 1995. Mobility of western flower thrips in tomato. *Thrips Biology and Management* (eds. Parker BL, Skinner M and Lewis T), pp.563-566. Plenum Press, New York and London.

Ramachandran S, Funderburk J, Stavisky J and Olson S. 2001. Population abundance and movement of *Frankiliniella* species and *Orius insidiosus* in field pepper. *Agricultural and Forest Entomology* **3**, 129-137.

Reddy IN, Nickle WR and Rao PN. 1982. Studies on *Howardula aptini* (Nematoda: Spaerulariidae) parasitic in *Megaluriothrips* sp. India. *Indian Journal of Nematology* **12**, 1-5.

Richards PC and Schmidt JM. 1996. The suitability of some natural and artificial substrates as oviposition sites for the insidious flower bug, *Orius insidiosus*. *Entomologia Experimentalis et Applicata* **80**, 325-333.

Sabelis MW and Van Rijn PCJ. 1997. Predation by insects and mites. *Thrips as Crop Pests* (ed. Lewis T), pp. 259-354. CAB International, Wallingford, UK.

Salguero Navas VE, Funderburk JE, Beshear RJ, Olson SM and Mack TP. 1991. Seasonal patterns of *Frankliniella* spp. (Thysanoptera: Thripidae) in tomato flowers. *Journal of Economic Entomology* **84**: 1818-1822.

Sharga US. 1932. A new nematode, *Tylenchus aptini* sp. n., a parasite of Thysanoptera (Insecta: *Aptinothrips rufus* Gmelin). *Parasitology* **24**, 268-279.

Smith FE. 1961. Density dependence in the Australian thrips. *Ecology* **42**, 403-407.

Teerling CR, Pierce HD, Borden JH and Gillespie DR. 1991. Identification of alarm pheromone in the western flower thrips, *Frankliniella occidentalis*. *Journal of Chemical Ecology* **19**, 681-697.

Teulon DAJ, Kolb TE, Cameron EA, McCormick LH and Hoover GA. 1993. Pear thrips, *Taeniothrips inconsequens* (Uzel) (Thysanoptera: Thripidae), on sugar maple, *Acer saccharum* Marsh: a review. *Zoology (Journal of Pure and Applied Zoology)* **4**, 355-380.

Teulon DAJ, Wouts WM and Penman DR. 1997. A nematode parasite of the New Zealand flower thrips (Thysanoptera: Thripidae). *New Zealand Entomologist* **20**: 67-69.

Tipping C, Nguyen KB, Funderburk JE and Smart Jr. GC. 1998. *Thripinema fuscum* n. sp. (Tylenchida: Allantonematidae), a parasite of the tobacco thrips, *Frankliniella fusca* (Thysanoptera). *Journal of Nematology* **30**: 232-236.

Toapanta M, Funderburk JE, Beshear RJ, Olson SM and Mack TP. 1996. Abundance of *Frankliniella* spp. (Thysanoptera: Thripidae) on winter and spring host plants. *Environmental Entomology* **25**, 793-800.

Tommasini MG and Nicoli G. 1993. Adult activity of four *Orius* species reared on two preys. *Bulletin of the International Organization of Biological Control/Western Pacific Region*, **16**, 181-184.

Tsai JH, Yue BS, Funderburk JE and Webb SE. 1996. Effect of plant pollen on growth and reproduction of *Frankliniella bispinosa*. *Acta Horticulturae*, **431**, 535-541.

Van de Wetering F, Van der Hoek M, Goldbach R and Peters D. 1999. Differences in tomato spotted wilt vector competency between males and females of *Frankliniella occidentalis*. *Entomologia Experimentalis et Applicata*, **93**, 105-112.

Van Rijn PCJ, Van Houten YM and Sabelis MW. 2002. How plants benefit from providing food to predators even when it is edible to herbivores. *Ecology*, in press.

Varley CG, Gradwell GR and Hassell MP. 1973. *Insect population ecology an analytical approach*. University of California Press, Berkeley and Los Angeles.

Venzon M, Janssen A, Pallini A and Sabelis MW. 2000. Diet of a polyphagous arthropod predator affects refuge seeking of its thrips prey. *Animal Behavior* **60**, 369-375.