INVASION BIOLOGY OF THRIPS

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Abstract   Thrips are among the stealthiest of insect invaders due to their small size and cryptic habits. Many invasive thrips are notorious for causing extensive crop damage, vectoring viral diseases, and permanently destabilizing IPM systems owing to irruptive outbreaks that require remediation with insecticides, leading to the development of insecticide resistance. Several challenges surface when attempting to manage incursive thrips species. Foremost among these is early recognition, followed by rapid and accurate identification of emergent pest species, elucidation of the region of origin, development of a management program, and the closing of conduits for global movement of thrips. In this review, we examine factors facilitating invasion by thrips, damage caused by these insects, pre- and post-invasion management tactics, and challenges looming on the horizon posed by invasive Thysanoptera, which continually challenge the development of sustainable management practices.

INTRODUCTION

Many species of thrips (order Thysanoptera) are preadapted to an invasive life style. These small, opportunistic, vagile, and ubiquitous insects are often only a few millimeters or less in length and generally yellow, brown, or black in color; their morphological appearance can range from nondescript to species with exaggerated secondary sexual characteristics. Eggs are laid either inside or outside of host material. Metamorphosis is complex, with two larval instars, a propupal stage, and up to two pupal stages, depending on the suborder. Approximately 5500 described species of thrips in two suborders encompass eight families. Tubulifera species lay eggs outside of host material, have two pupal stages, and are all placed in a single family, the Phlaeothripidae. Terebrantia species lay eggs inside plant tissue, have one pupal stage, and are distributed across seven families. Thrips occupy widely disparate niches resulting in the manifestation of a diverse array of life styles. Phytophagous thripids, such as *Scirtothrips* spp., can exploit immature foliage, mature leaves support *Heliothrips haemorrhoidalis*, and senescing leaves can be utilized by *Selenothrips rubrocinctus*. Flower feeding is common among members of the Melanthripidae, Heterothripidae, and less advanced members of the Aeolothripidae. *Frankliniella* and *Thrips* spp. (Thripidae: Thripinae) are leaf and flower feeders with proclivities for facultative predation.

Members of the Phlaeothripidae can induce leaf galls (e.g., *Gynaikothrips ficorum*). The impressive *Idolothrips spectrum* (Phlaeothripidae) specializes on fungal spores, and most of the Merothripidae feed on fungal hyphae. Some important generalist natural enemies are obligate predators [e.g., *Franklinothrips* spp. (Aeolothripidae)], and an ectoparasitic existence has evolved at least once [e.g., *Aulacothrips dictyotus* (Heterothripidae)]. About 50% of the known species of Thysanoptera feed on fungi, approximately 40% feed on living tissues of dicotyledonous plants or grasses, and the remainder exploit mosses, ferns, gymnosperms, cycads, or are predatory (68, 108, 115). Intertwined with this astonishingly broad range of life styles is an inherent opportunism that allows many species to readily adopt and utilize a variety of resources in ephemeral and/or stable habitats.

Such gustatory flexibility and habitat infidelity is possible because many thrips species are generally not constrained by highly specialized evolutionary relationships with particular species of host plants, fungi, or prey. Monophagy is not uncommon, but polyphagy undoubtedly predisposes certain species as potential invaders (115). Consequently, when accidentally or purposely relocated to new areas with suitable environments, some species of thrips have the potential to establish, proliferate, and spread in their new range. Thus, invasion may occur because opportunistic thrips species can potentially utilize a variety of resources that fluctuate in availability both temporally and spatially. If in the new range thrips do not cause recognizable damage to agricultural crops or threaten native plants, they may remain unnoticed because of their unassuming size and the difficulty of detection and identification; thus successful invasion may occur without remark.

FACTORS FACILITATING INVASION BY THRIPS

We consider species of thrips to be successful invaders if they cross major geographical barriers with or without human assistance and establish and build self-sustaining populations in previously uncolonized regions. Major economic damage resulting from establishment, proliferation, and spread is not requisite for classification as a successful thrips invader, because some species, such as spore and fungal feeders, can invade natural areas and infiltrate existing food webs. The magnitude of subsequent ecological perturbations is often unknown, as these systems are of little economic significance and are usually poorly studied. Invasion success depends on the intensity of introduction into new areas (i.e., incursion frequency and numbers of pioneers entering); biological attributes of the invader (especially reproductive modes and capacity for increase); features of the ecosystem in which incursion has occurred; and the strength of the interaction between pioneer pressure (98), environmental conditions at the time of arrival (124), the invader's autecology, and the characteristics of the receiving ecosystem (51, 167).

Introduction Pathways and Establishment

Frequently, successfully established nonnative thrips species are introduced accidentally, repeatedly, and discontinuously over long periods from one or more ranges into new areas (50, 122, 159). Over a 13-year period (1980–1993), 43 terebrantian and 12 tubuliferan species were recorded entering The Netherlands on internationally traded produce from 30 countries (159). In the United States approximately 1000 thrips specimens are intercepted annually by border inspectors and sent to the Systematic Entomology Laboratory, USDA, for identification. Over a 16-year period (1983–1999), 130 thrips species from these samples were intercepted in plant shipments and 85% of contaminants comprised 23 species (122, 124). Sampling of plant material imported into Switzerland showed that 20% of cuttings and 12% of plants were infested with one thrips species, *Frankliniella occidentalis* (34). In the United States, 5% of introduced insect species that have established are thrips, but Thysanoptera constitute only 0.8% of known native insect species (73), and in California 16% of the cataloged thrips fauna is exotic (60). In New Zealand, 24 of 51 (47%) known species of terebrantian thrips are exotic and similar high numbers of exotic thrips species are common in the South Pacific Islands, and in some instances all known thrips species are exotic (e.g., Kiribati) (117). Some species of thrips are wingless, but this limitation does not preclude invasiveness given the frequent importance of human involvement in pest movement. For example, *Aptinothrips rufus*, a wingless, grass-living thrips from Europe, is one of the most widespread insects in the world (107, 110), and its congener, *A. stylifer*, has been found at 3500 m in the Swiss Alps. The potential for repeated unintended introductions of thrips through international trade is well documented and undoubtedly has contributed to their high invasion success, especially in the case of polyphagous species.

Variation in repeated initial introductions can enhance the gene pool of founding populations, and temporally stratified introductions are more likely to coincide with benign environmental conditions that ease barriers to establishment (76). Following establishment, secondary releases spread species within the new range and, if human-mediated, may occur repeatedly. Crop cultivation is a major vector for both primary introduction and secondary dispersal of thrips pests. Farming and horticultural practices mitigate impeding environmental hazards, allowing the persistence of minimum viable populations in areas outside of their expected range, and spread is enhanced and accelerated because of careful human management and redistribution of infested crops that enable pioneers to overcome establishment barriers. As a result, strong spatial correlations between cultivation and pest invasion often exist (91).

Rapid, long-distance transport of thrips as stowaways in agricultural produce has greatly expanded the range and pest status of many species and has enabled short-lived males of bisexual species to survive and reproduce in new areas. The implications of increased genetic variability on pest status and subsequent control are most likely considerable (76, 115). During transportation, thigmotactic adults

and larvae of pests of commercial crops are easily concealed under bracts, in buds, within leaf bases, or along leaf veins. Eggs embedded in plant tissue make detection and identification of motile stages by nonspecialists difficult, as well as elimination with insecticides problematic (85, 108).

Numerous examples of thrips as successful invaders exist. The Roman armies likely took *Thrips tabaci* with them as contaminants in their onions and garlic wherever they went (110). *Thrips simplex*, probably native to southern Africa, has moved globally with the international trade in gladiolus bulbs (85). *Chaetanaphothrips* spp. have moved widely in tropical climates with orchid production, and *Hercinothrips femoralis* and *Chaetanophothrips signipennis* are common in banana plantations around the world (84, 86). Many grass-inhabiting thripids such as *Aptinothrips*, *Chirothrips*, and *Limothrips* species have been carried worldwide as pupae within bracts surrounding grass seeds, or as adults within straw, hay, or the soil ballast of sailing ships (107, 108). Global trade in ornamental greenhouse plants rapidly spread a highly pestilential strain of *Frankliniella occidentalis*, a species native to the southwestern United States and vector of tospoviruses, around the world beginning in the mid-1980s (108, 115), and small populations are continuously being reintroduced from invaded areas back into the native U.S. range (123). Pest species from tropical or subtropical areas can be transported into environmentally hostile regions. There they may survive in the greenhouse environment where propagation of infested host plants eliminates climatic barriers to establishment (e.g., *H. haemorrhoidalis* in Europe). Greenhouses may also provide important overwintering sites from which outdoor populations establish in spring to attack vegetable crops (e.g., *Thrips palmi* in Japan and *F. occidentalis* in Ontario, Canada). Conversely, thrips pests of tea, tobacco, grapes, and currants, of which the commercial products are dried and packaged, are less likely to be transported globally because preparation for shipment is an effective disinfestant (85, 108, 115).

Experimental results indicate that the probability of establishment increases with pioneer population size and that growth rates of incipient infestations are positively correlated with the number of founders (43, 98). Together, these factors override the negative impacts of demographic stochasticity, Allee effects, and genetics (e.g., inbreeding depression) (43). For example, 33% and 100% of founding populations of 10 and 810 individual *Sericothrips staphylinus*, respectively, established on the weed gorse, *Ulex europaeus*, in New Zealand (98). Leaves and fruit from plants infested with adult thrips can easily harbor sufficient eggs to give rise to larval populations exceeding the minimum viable population sizes needed for establishment (54). In addition, persistence can be independent of initial population size and is influenced by density-independent factors such as weather (124) and the size and stability of the habitat patch. Biological drivers such as a high intrinsic rate of increase can allow small founding populations to increase quickly, thereby minimizing the threat of extinction due to stochastic events. Under such conditions, insect populations may establish from one mated female (43). However, invasions by thrips usually result from a complex and often unpredictable interplay of biological, ecological, and anthropogenic mechanisms.

THRIPS AS PEST SPECIES

Of an estimated 8000 extant species of thrips (85) and more than 5500 species
that are described, scarcely 1% are recorded as serious pests. A large part of the
economic literature deals with just four species, *Thrips tabaci*, *Frankliniella occi-
dentalis*, *Scirtothrips dorsalis*, and *T. palmi* (109, 115). Thrips can be pestiferous
in various ways: as irritants to field workers or the public, as contaminants in a
variety of situations, by direct plant damage affecting yield or cosmetic appear-
ance, as vectors of plant diseases, and as perceived quarantine risks that negatively
impact trade. When large numbers are present they can be quite irritating; some
species "bite," causing an itching and pricking sensation that may provoke rashes
or inflammation in the ears and nose (84). In northern Queensland a school was
forced to curtail outdoor activities after mid-morning because vast numbers of a
local population of thrips, *Pseudanaphothrips araucariae*, were causing distress to
children, infesting their hair and food (114). An estimated 100 to 150 million grain
thrips, weighing 4 to 6 kg, emigrate daily from 10 ha English wheat fields over a
typical 7- to 10-day period as the crop senesces (85). Few species can penetrate hu-
man skin and suck fluids but probably not blood, as previously reported (65, 164).
Some species of thrips are associated with stormy weather (84), and an informal
survey by Kirk (72) showed that the common name for thrips in seven countries
in Europe includes reference to thunderstorms (e.g., storm flies and thunder flies).
Careful study of the effect of weather on mass flights of thrips, however, showed
that frontal conditions and incipient thunderstorms actually discouraged the mass
flight of thrips and resulted in high densities 1 to 2 m above ground, resulting from
attempts at landing (67, 82, 83).

Because of their small size, ability to build to high numbers, cryptic behavior,
egg deposition inside plant tissue (e.g., all Terebrantia), and a propensity to secrete
themselves in tight spaces, thrips can contaminate a wide variety of commodities
and human devices. Analysis of contaminants in samples of four unground spices
collected from 56 regions around the United States showed that thrips were present
in an average of 34.2% of multiple 10- to 50-g samples (ranging from 4.8% for
unground sage to 54.1% for unground thyme) (37, 38). Levels in ground samples of
these same four spices plus five others averaged only 2.8% (ranging from 0.2% for
ground paprika to 7.7% for ground oregano), probably because thrips fragments
were more difficult to identify after the spices had been processed. Thrips can also
serve as vectors of bacteria or fungi in plant cell cultures, and the rapid spread
of contamination in specific growth rooms is often indicative of the presence
of either mites or thrips (13, 15, 74, 79). The thigmotactic behavior of thrips
sometimes results in substantial numbers entering smoke detectors, resulting in
false fire alarms, and thrips have been found in factory-sealed hypodermic needles
and tampons (111, 127, 144).

Several species of thrips are well known for causing plant damage and re-
ductions in crop yield. On 12 selected field crops, feeding by Thysanoptera re-
sulted in an estimated 43% average yield loss (range of 3–13% in Swedish rye
to 100% in Kenyan tea) (85). Several crops are severely impacted by the same

thrips species throughout the world almost wherever that crop is grown. *Thrips tabaci* is a cosmopolitan pest of onions grown between sea level and 2000 m, and *Chaetanaphothrips signipennis* is found on bananas in Africa, Australia, Fiji, and Central and South America (84). Sixteen species of thrips are commonly found on cotton grown in various areas of the world, 12 of which cause significant damage (80). Cowpea is one of the most important staple crops in Africa, and the African bean thrips *Megalurothrips sjostedti* causes significant yield loss over much of the dry savanna region of West Africa (155). *Scirtothrips perseae* was introduced into California in 1996 and by 1998 had spread throughout most of the avocado-growing region, resulting in a 12% reduction in grower revenues. Initial impacts on producers were estimated to be $8.7 million per year (57).

Many species of thrips affect the cosmetic quality of a commodity such that economic returns can be severely impacted. California citrus is grown for the fresh market and is marketed on the basis of visual appeal with minimal or negative grower returns from processed fruit. Despite studies showing that *Scirtothrips citri* surface scarring has no impact on fruit quality, annual pesticide treatments cost California growers well in excess of $11 million per year (6, 105). Cosmetic thresholds are similarly low for damage caused by thrips on a wide variety of fruits, vegetables, flowers, and indoor plants (23, 24, 85).

In addition to direct or cosmetic plant damage, thrips vector a number of microbial pathogens through mechanical transmission (152). Thrips also transmit viruses belonging to at least four virus groups, ilarviruses, sobemoviruses, and carmoviruses, which are all pollen-borne, and tospoviruses, in which there is a more intimate biological relationship between the virus and thrips vector, involving leaf-to-leaf transmission (151, 163). Tospoviruses are now recognized worldwide as limiting factors in the production of a large number of horticultural crops, and the tomato spotted wilt *Tospovirus* has a known host range of 1090 species in 85 plant families (20, 131, 134). Thrips are the only known vectors of tospoviruses, but only 0.16% of the known Thysanoptera (10 of 5500) have been implicated in transmission (109, 110). These vector species are not closely related, which suggests that either many thrips species have lost an association with tospoviruses or that many *Tospovirus* species have evolved an independent relationship with a thrips species (109). It is interesting that thrips can acquire tospoviruses only during a well-defined period during the first and early second instars when there is a temporary association between the *Tospovirus* and the thrips alimentary system, in particular, the midgut, visceral muscles, and salivary glands (100).

In some cases, thrips can have a large impact on international trade. As listed above, thrips are pestiferous in diverse ways and across a broad spectrum of commodities. Thus, it is not surprising that they are a focus for quarantine inspectors and can cause serious economic impacts by reducing potential trade, often in contrast with their minimal impact on similar commodities within their native range (64, 73, 95, 110, 159, 160).

BIOLOGICAL ATTRIBUTES OF INVASIVE THRIPS

Invasion biologists have sought unsuccessfully to identify key biological features that are likely to predispose insect species as successful invaders and that can be used to consistently predict invasion likelihood (75, 92, 165). However, invasive thrips species appear to have several general biological traits in common. Thrips that are successful invaders are typically abundant in the region of origin, exhibit high levels of vagility (i.e., natural or human assisted), and have close association with human activity (e.g., farming or trade). Following translocation, pioneers can rapidly synchronize life cycle characteristics with the new environment (important for transhemisphere introductions), and they often lack obligate diapause and are multivoltine and polyphagous. Many successful invaders exhibit high fecundity and short generation times, often with a predisposition to parthenogenesis, precluding the need to find mates under low-density populations or when shorter lived males die during transit of an infested commodity. In some cases, combinations of these attributes promote a propensity to rapidly develop insecticide resistance (73, 108, 112, 115, 140, 165).

These biological characteristics are exhibited by successful invasive and economically destructive species in three genera, *Frankliniella*, *Scirtothrips*, and *Thrips* (all Thripidae: Thripinae). *Frankliniella* and *Scirtothrips* are particularly problematic given that many species in these genera remain to be identified. However, predicting invasion and pest status on the basis of congeneric association is imprecise (92, 165). For example, *T. palmi* emerged as a major pest of cucurbits and solanaceous crops in 1978 in Japan and rapidly spread around the world causing severe economic damage (108). Congeners in Asia with similar biologies might be expected to have high invasion and pest potential on the basis of the behavior of *T. palmi*, but this has not been observed (108). The abundant and widespread Australian plague thrips, *T. imaginis*, has not spread from Australia into New Zealand despite repeated introduction on winds (116). Similarly, the pestiferous and polyphagous New Zealand native *T. obscuratus* has not crossed the Tasman Sea to establish in Australia or elsewhere despite infesting a multitude of crops exported from New Zealand (115) and having been intercepted on said exports (50).

Biotypes, strains, or races of the same species, and their associated genetic underpinnings, may promote invasiveness in some thrips species. For example, the evolution of insecticide-resistant strains of *F. occidentalis* was correlated with its global rise as a major pest while monophagous nonpestiferous strains resided innocuously in several countries (e.g., New Zealand in lupine flowers), often for many years prior to the invasion of the polyphagous pest biotype (73). Conversely, a succulent-feeding strain of *Scirtothrips aurantii* from South Africa has recently established in Australia on the mother-of-millions weed (*Bryophyllum delagoense*) but has not been recorded to attack citrus or mangoes in its new range (104), unlike conspecifics in the native range that are highly pestiferous on these crops

(59). The genetic basis for biotype formation is not well understood and deserves research attention. Biotypes of some species, such as *F. occidentalis*, can exist as monophagous and polyphagous strains, both of which have invaded successfully. On the other hand, radically different biotypes of *T. tabaci* and *T. palmi* do not appear to exist, and the biology of these pests appears to be relatively uniform across invaded areas (108).

Ecosystem Attributes Facilitating Invasion

To persist in a new range, thrips must exhibit population growth rates that enable the incipient population to overcome barriers to permanent establishment and spread. Three factors influence an invader's growth rate: (*a*) resources, (*b*) natural enemies, and (*c*) the physical environment (the role of climate has been discussed above) (139).

Resource Utilization

Successful resource exploitation occurs if resources are abundant, if access to resources is unhindered, if the invader has a superior rate of resource acquisition, or if the invader requires few contested resources to achieve high per capita growth rates (139). The greater pest status of the bisexual *F. occidentalis* than of the thelytokous *T. tabaci* in greenhouse-grown cucumbers in Europe was not due to significant differences in biotic drivers, such as intrinsic rate of increase, net reproductive rates, or developmental times, but most likely to superior resource acquisition (158). It has been hypothesized that *F. occidentalis* may outperform *T. tabaci*, thereby displacing it in greenhouses, by being a more efficient exploiter of pollen in this environment owing to its specialized pollen-feeding habit. In addition to feeding on pollen and plant tissue, adult *F. occidentalis* can supplement their diet with high-protein resources by feeding on other herbivores such as spider mite eggs (150) and thrips larvae (158). In addition, predation rates can increase as host plant quality deteriorates (1). The omnivorous habits of *F. occidentalis* may provide it a competitive advantage over *T. tabaci* in greenhouses given that the variety of food sources available for use and reproductive output of *F. occidentalis* may exceed that of *T. tabaci* when resources such as pollen and prey are available. However, thrips with narrow dietary breadths can also establish in new areas and become pestiferous. *Scirtothrips perseae*, a pest of commercially grown avocados in California, is native to Mexico and Central America. This apparently monophagous thrips was likely imported repeatedly at irregular intervals on illegally imported plant material since its first detection in 1971 and eventual establishment in California in 1996 (53, 61). This species has unique access to succulent young avocado foliage in California, as competing thrips species are lacking for this resource. This is not the case in the home range of *S. perseae*, where *Neohydatothrips burungae* competes for resources and is as common as *S. perseae* on immature avocado leaves in some areas (61).

Resident Natural Enemies

Invasion opportunities can arise when natural enemies (i.e., predators, parasitoids, parasites, and pathogens) fail to accompany the invader from its home range. In addition, the receiving ecosystem may lack either specialist or generalist natural enemies that can vigorously exploit the invader as a resource to either inflict sufficient mortality or reduce resource acquisition to a level that retards population growth (71, 139, 149). Several factors impede the success of resident natural enemies in controlling invasive thrips of economic importance. First, invading thrips species typically lack specialist natural enemies in the receiving ecosystem that respond rapidly in a density-dependent manner to inflict high levels of mortality. Most resident natural enemies that attack thrips are generalist predators [e.g., phytoseiid mites (*Neoseiulus* spp.) and predatory thrips (*Franklinothrips* spp.)] that feed on a variety of arthropods in addition to thrips (62, 63). Second, fungal entomopathogens [e.g., Neozygitaceae: *Neozygites* spp. and Hypocreaceae: *Verticillium* spp.] rarely cause regular natural epizootics that regulate populations, even though some species such as *Entomophthora thripidum* and *N. parvispora* are restricted to thrips species (19). Third, specific natural enemies such as hymenopteran parasitoids that attack thrips eggs (e.g., Mymaridae: *Megaphragma* spp.) and larvae (e.g., Eulophidae: *Ceranisus* spp.) generally inflict low levels of mortality. These parasitoids tend to be specific to the subfamily level, rarely to genus, and do not appear to be major regulators of thrips population growth. Similarly, parasitic nematodes that specialize on thrips [e.g., *Thripinema* spp. (Tylenchida: Allantonematidae)] retard oogenesis in females but fail to alter growth rates, and it is doubtful whether these parasites regulate thrips population growth in the field (86, 89). No viral diseases of thrips are known.

Fourth, the life cycle of thripids minimizes life stage exposure to any single generalist natural enemy species. Typically, eggs are oviposited within plant tissues; there are two exposed feeding larval instars, two pupal stages that pupate within protective cracks on branches or in soil beneath the host plant, and winged vagile adults. Under such conditions, a guild of generalist natural enemies would need to be simultaneously available in several distinct habitats (e.g., arboreal to attack thrips larvae and adults exposed on leaves, and subterranean to attack pupal stages in the soil) to minimize the number of life stages benefiting from refuge in natural enemy free space. In addition, the "boom and bust" ecology, patchy distribution of high-density populations, and occurrence of life stages that occupy widely varied niches make invasive thrips an unstable resource for resident natural enemies. Thus, thrips apparency fluctuates greatly, making temporal and spatial occurrence unpredictable (63). Fifth, the defensive behavior of some thrips (e.g., anal exudates), combined with environmental complexity, can reduce the attack success of natural enemies (9, 55, 56).

Consequently, resident natural enemies that fail to regulate invading thrips numbers permit the development of large populations that can act as donors invading new areas, thereby failing to limit the geographic range of the invader (52). When

coupled with benign environmental conditions, especially climate, this further fails to impede initial establishment or subsequent spread of an invading thrips species (8).

MANAGEMENT OF INVASIVE THRIPS

Inspection and Treatment of Imported Commodities

The simplest means of dealing with a potentially invasive and pestiferous thrips is to prevent entry and establishment into nonendemic regions. The North American Free Trade Agreement (NAFTA) and the General Agreement on Tariffs and Trade (GATT) have significantly altered the enforcement of Sanitary and Phytosanitary Standards (SPS) (41, 145). To date, it appears that the World Trade Organization's SPS agreements favor exporters and establish limitations on environmental protection and plant safety restrictions (3, 120, 144). Australia, Chile, New Zealand, and Japan are recognized for their extreme rigor in attempting to prevent new pest introductions via commodity imports. This used to be the case in the United States prior to USDA-APHIS' mandated transition in 1995 from an organization that focused on protecting agriculture to an agency that also emphasizes enhancing marketability of agricultural produce (106, pp. 2–5). More recently, the United States' shift to a focus on homeland security in response to terrorism threats is expected to further erode plant and animal quarantine inspection capability by diverting the focus of some of a limited number of commodity inspectors to security issues.

Methyl bromide is currently used worldwide for the post-harvest disinfestation of a number of commodities either by the exporting or importing country when a thrips infestation is discovered. For example, Australia routinely fumigates citrus from the United States with methyl bromide when *Caliothrips fasciatus* is found. This species has a propensity to overwinter as adults inside the navel of navel oranges shipped from California. A search of the current USDA-APHIS Treatment Manual shows eight treatment schedules involving various species of thrips and commodity combinations, and all stipulate disinfestation treatment with methyl bromide (153). This manual lists several other approved chemical (phosphine and sulfuryl fluoride fumigation and treatments with aerosols/micronized dusts and chemical dips, dusts, and sprays) and nonchemical treatments (hot-water immersion, steam, vapor heat, forced hot air, cold treatments, and irradiation) for various commodities (153). Some of these treatments might treat thrips as one of several commodity contaminants, but in no case are thrips listed as a target species. International protocols for disinfestation of various thrips species also rely heavily on methyl bromide (see the International Plant Protection Convention web site at https://www.ippc.int/IPP/En/default.jsp). As worldwide methyl bromide use is phased out, alternative disinfestation procedures must be developed. Pest management prior to harvest and/or insecticidal dips after harvest are obvious methods of control (49). The Food and Drug Administration and USDA-AHPIS approved

irradiation to disinfest fresh foods in the United States in 1986 and 1989, respectively. Hawaii became the first location in the world to use irradiation as a commercial quarantine treatment for fresh fruits when a commercial e-beam/converted X-ray facility became operational on the island of Hawaii in July 2000 (119). Other treatments that have shown promise for thrips disinfestation but require further research prior to implementation include low-temperature storage or low temperature combined with use of sulfur dioxide pads; treatment with vapor heat; use of volatile plant aldehydes; fumigation with hydrogen cyanide, methyl iodide, or ozone gas; and use of controlled atmospheres of various types (21, 47, 48, 78, 135, 154, 161, 169, 170).

Biological Control

Density-dependent regulation of thrips populations by upper-trophic-level organisms is highly controversial (4), and limited field evidence exists supporting top-down regulation of pest thrips populations (36). No effective classical or inoculative biological control programs (i.e., projects that deliberately imported and established natural enemies from the invader's home range into the invaded range) against exotic thrips species have been documented with solid field data demonstrating significant natural enemy impact (61, 63 121). The best-known attempt at classical biological control of an invasive pestiferous thrips has been the use of *Thripobius semiluteus* against *H. haemorrhoidalis* in California, Israel, and New Zealand (35, 97, 166). More than 60 years of effort have gone into establishing biological control agents of *Thrips tabaci* in many areas of the world, with limited success (132).

Much research attention has been focused on augmentative biological control (i.e., deliberate periodic introductions of mass-reared natural enemies into cropping systems) for the suppression of pest thrips in both indoor and outdoor crops. Thripid pests of greenhouse-grown ornamentals and vegetables and ornamentals in interiorscapes have been controlled to some extent with releases of phytoseiid mites (e.g., *Neoseiulus cucumeris* against *F. occidentalis* in cucumbers; 39), anthocorid bugs (143), predaceous nematodes, or combinations of these (136). However, problems related to temperature, humidity, day length, and prey size can limit natural enemy effectiveness (25, 157). Loomans (88) searched widely for parasitoids that might be useful in biological control of thrips pests in Dutch greenhouse vegetables and ornamentals but concluded that known species showed limited potential for either inoculative or inundative control. Fungal pathogens, in particular, *Beauveria bassiana*, *Metarhizium anisopliae*, *Paecilomyces fumosoroseus*, and *Verticillium lecanii*, have been evaluated for use against various thrips in outdoor and indoor crops either alone or in combination with other natural enemies or insect attractants. Research in this area, particularly for application in greenhouses, is promising (32, 90). However, temperature, fungal species, and strain of fungus used for thrips suppression have major affects on efficacy and, in general, results have suffered compared with grower reliance on relatively

inexpensive insecticides (22, 31, 32). Sprays of *B. bassiana* can significantly reduce *F. occidentalis* populations on cucumbers and are compatible with augmentative releases of phytoseiid mites (70).

Augmentative biological control of thrips in outdoor crops has been unsuccessful owing to a lack of cost-effective natural enemies available for purchase; well-researched release strategies; and knowledge regarding release timing, numbers to release, and the need for alternative food sources during periods of target prey scarcity (62, 63). Effective thrips management programs that utilize natural enemies as part of an integrated pest management program in both indoor and outdoor crops require strategies that combine several management techniques such as selective insecticides and good hygiene to enhance the efficacy of biological control agents (69, 129, 132, 138).

Cultural Control

Cultural controls are techniques developed from crop management or mechanical practices that can be readily manipulated to disadvantage pest population growth while having limited adverse effect on crop productivity. The use of composted organic yard waste has been investigated as a strategy for disrupting pupation of *Scirtothrips perseae* larvae by promoting an antagonistic microarthropod, nematode, and fungal fauna under avocado trees (58). Ground covers have been manipulated to promote populations of phytoseiid predators in citrus orchards for control of *S. citri* (40), and wind-break pollen has been used to increase resident populations of *Euseius addoensis addoensis* for control of *S. aurantii* in South African citrus orchards (44). Cultural control strategies have not been widely adopted for thrips management in outdoor crops, but techniques based on sanitation (e.g., screen meshes over intake vents to exclude immigrants and roguing infested plants) and manipulation of the indoor environment are employed more rigorously in the greenhouse industry because of the higher value of these crops, smaller areas that require treatment, and greater practicality of implementation (69). Thrips are among the smallest of greenhouse pests and the screen size required to restrict their movement into a greenhouse often hinders air movement and leads to undesirable increases in temperature and humidity (10–12, 27). Reflective foils, paints, or synthetic mulches have been evaluated to deter thrips movement onto plants, but their effectiveness is low, their cost high, and photodegradable synthetic mulches that eliminate the need to remove and dispose of the plastic at the end of the season tend to degrade prematurely (11, 42, 96, 142). Ultraviolet-absorbing plastic films covering greenhouses appear to interfere with thrips orientation behavior, but their applied use is still under evaluation (5, 26, 27). Sprays of jasmonic acid, a natural plant defense elicitor, reduced *Frankliniella occidentalis* feeding on cotton but this technology requires further testing prior to commercial implementation (126). Utilization of multiple cultural techniques such as cover crops, modification of tillage practices, and removal of alternative weed host plants has also been largely ineffective in managing pest thrips (45, 66).

Crop Breeding

As the pressure to reduce pesticide use increases and better breeding methods
utilizing manipulative molecular methods are developed, the economic viability
and incentive to develop and use resistant plant varieties for insect management
may increase (14, 30, 168). Several authors have noted that improvements in crop
breeding and other molecular technologies will likely form the cornerstone of
future management for the many serious *Tospovirus* diseases that are vectored by
thrips (28, 77, 163). To date, vector control has been ineffective and only with
the integrated use of moderately resistant cultivars, chemical control, and cultural
practices, have wilt epidemics been managed effectively. Substantial research has
focused on evaluating field or vegetable crop plant varieties tolerant or resistant
to thrips, but with some exceptions progress has been slow (2, 16, 33, 99, 141).
Similarly, few floriculture varieties with resistance to thrips are currently in use by
flower and nursery plant producers, who still depend largely on chemical control
for thrips management (29, 125, 162).

Chemical Control

The most common methodology used for dealing with pestiferous thrips is chem-
ical control, which is usually the first method considered when a newly invasive
and economically important thrips is discovered (85). Unfortunately, owing to the
cryptic nature of thrips and the difficulty in monitoring incipient infestations, there
are relatively few examples in which a newly introduced thrips species has been
discovered soon after introduction such that eradication is attempted and success-
ful. One exception was the detection and eradication of *Thrips palmi* in southern
England in April 2000 during a routine inspection of ornamental chrysanthemum
flowers in a commercial greenhouse (93). The outbreak was confined to two (2.1
and 2.5 ha) glasshouses that specialized in production of chrysanthemums using
imported cuttings. Eradication using insecticide treatments, methyl bromide soil
sterilization, and imidacloprid-treated compost cost the grower £56,000 from April
2000 to July 2001. The 2004 economic impact of *T. palmi* had it established in
England was estimated to be between £16.9 and £19.6 million over a 10-year pe-
riod, depending on its rate of spread. It is unclear to what degree revenue from
English exports liable to carry *T. palmi* might have been lost, but the benefit-to-cost
ratio for this eradication was estimated to be between 4:1 and 9:1 if there was no
loss of exports and between 95:1 and 110:1 if significant export losses had resulted
from *T. palmi* establishment and spread (93).

Future Management of Invasive Thrips Species

Many countries around the world remain vigilant in monitoring for and attempting
to eliminate invasive species. However, with increasing international trade, relax-
ation of trade barriers, increasing air travel, and international movement of greater
numbers of people, we speculate that invasive thrips species will continue to be

found in new regions of the world, probably at a high rate similar to that seen over the past 20 years. Although some countries continue to invest heavily in border inspectors, in the United States the focus on protecting agriculture has shifted to protecting homeland security and far fewer inspectors than in the past are asked to oversee an increasingly difficult volume of shipments. One solution to this problem may be the development and implementation of automated imaging systems that screen large volumes of baggage, packages, or even metal shipping containers (81, 94, 133, 147). In addition, worldwide electronic communication, increasing numbers of journal articles and illustrated taxonomic keys available on-line or as easily transported compact discs that are laptop operable, and searchable pest interception and molecular databases may dramatically improve the rapidity of identification of quarantine thrips species when they are first detected (7, 101, 104, 156).

Thrips are not an easy group of insects to identify, as many of the most pestiferous genera exhibit a bewildering phenotypic plasticity of key traits (e.g., *Scirtothrips* and *Frankliniella* spp.) or simply lack good characters for identification (e.g., *Haplothrips* spp.). Worldwide, relatively few taxonomists, especially young emerging taxonomists, specialize in thrips identification and phylogeny. Thysanoptera descriptive taxonomy is critical as is its integration with in-depth biological studies needed to understand evolutionary processes and the ecological diversity of this order (108, 110). Many quality ecology, biology, or pollination studies have been conducted on various thrips species without the concurrent storage of voucher specimens, later leading to questions regarding the identity of the species or species complex that was investigated (110, 128). Molecular methodologies are likely to dramatically change the future of thrips systematics (103, 113), and we are only beginning to realize that there are host-associated strains of particular thrips species that may evolve new plant associations after invading new regions of the world (17, 104). Genetic analysis will also be used increasingly to resolve taxonomic disputes related to potentially invasive thrips (87, 118), and molecular analyses have the potential to assist in rapidly identifying thrips intercepted at quarantine stations, even if only immature stages or dead specimens are found (18, 102, 137, 148). Similar molecular-based techniques can be used to determine the likely native range of invasive species and to estimate when and how many introductions may have occurred. For example, molecular analyses have indicated that the origin of the invading population of *S. perseae* in California is almost certainly central Mexico, even though this pest has a range extending into central Guatemala. Genetic engineering of crop plants or thrips endosymbionts may provide useful management tools for invasive thrips pests and the disease-causing organisms they vector. This technology could greatly reduce reliance on broad-spectrum pesticide use for thrips control.

CONCLUSIONS

New thrips species with the propensity to become global invaders that attack important agricultural crops will undoubtedly emerge from obscurity and force this group of insects to even greater notoriety. We expect that in the near future, numerous

thrips species will emerge to join the resident pest phalanx and will exhibit high invasion potential as novel crops and growing strategies are introduced, quarantine practices are changed, and the pace of international commerce increases. Serious challenges can be expected for managing incursive thrips. Perhaps one of the most important is the need to train specialists who can rapidly and accurately identify thrips using both morphological and molecular techniques while having an appreciation of thrips biology and ecology. Molecular tools need greater adoption for disentangling species complexes and for resolving synonymies. Greater attention needs to be given to developing management strategies that are not straight-jacketed by the use of insecticides. Plant breeding, especially the development of transgenic plants, may offer integrated pest management programs a much needed tool to manage thrips that exhibit tendencies to rapidly develop insecticide resistance and for managing diseases caused by tospoviruses vectored by thrips. Genotyping invading species may provide greater opportunities for prospecting for specialist natural enemies in the invader's native range and may increase the efficacy of thrips biological control. We envision many interesting and frustrating research problems on invasive Thysanoptera only now are crossing the horizon.

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LITERATURE CITED

1. Agrawal AA, Kobayashi C, Thaler JS. 1999. Influence of prey availability and induced host-plant resistance on omnivory by western flower thrips. *Ecology* 80:518–23

2. Alabi OY, Odebiyi JA, Jackai LEN. 2003. Field evaluation of cowpea cultivars (*Vigna unguiculata* [L.] Walp.) for resistance to flower bud thrips (*Megalurothrips sjostedti* Trybom) (Thysanoptera: Thripidae). *Int. J. Pest Manag.* 49:287–91

3. Anderson K, McRae C, Wilson D, eds. 2001. *The Economics of Quarantine and SPS Agreement*. Adelaide: CIES-AFFA Biosecurity Aust.

4. Andrewartha HG, Birch LC. 1954. *The Distribution and Abundance of Animals*. Chicago: Univ. Chicago Press

5. Antignus Y. 2000. Manipulation of wavelength-dependent behavior of insects: an IPM tool to impede insects and restrict epidemics of insect-borne viruses. *Virus Res.* 71:213–20

6. Arpaia ML, Morse JG. 1990. Citrus thrips, *Scirtothrips citri* (Moulton) (Thys., Thripidae) scarring and navel orange fruit quality in California. *J. Appl. Entomol.* 111:28–32

7. Bailey W. 2004. Coming soon to your network: the PPQ global pest and disease database. *CPHST News* 1:4

8. Baker RHA. 2002. Predicting the limits to the potential distribution of alien crop pests. See Ref. 46, pp. 207–41

9. Bakker FM, Sabelis MW. 1989. How larvae of *Thrips tabaci* reduce the attack success of phytoseiid predators. *Entomol. Exp. Appl.* 50:47–51

10. Bell ML, Baker JR. 2000. Comparison of greenhouse screening materials for excluding whitefly (Homoptera: Aleyrodidae) and thrips (Thysanoptera: Thripidae). *J. Econ. Entomol.* 93:800–4

11. Berlinger MJ, Taylor RAJ, Lebiush-Mordechi S, Shalhevet S, Spharim I. 2002. Efficiency of insect exclusion screens for preventing whitefly transmission of tomato yellow leaf curl virus of tomatoes in Israel. *Bull. Entomol. Res.* 92:367–73

12. Bethke JA, Paine TD. 1991. Screen hole size and barriers for exclusion of insect pests of glasshouse crops. *J. Entomol. Sci.* 26:169–77

13. Bhagwhat B, Lane WD. 2003. Eliminating thrips from in vitro shoot cultures of apple with insecticides. *HortScience* 38:97–100

14. Birch RG. 1997. Plant transformation: problems and strategies for practical application. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 48:297–326

15. Blake J. 1988. Mites and thrips as bacterial and fungal vectors between plant tissue cultures. *Acta Hortic.* 225:163–66

16. Bowman DT, McCarty JC Jr. 1997. Thrips (Thysanoptera: Thripidae) tolerance in cotton: sources and heritability. *J. Entomol. Sci.* 32:460–71

17. Brunner PC, Chatzivassiliou EK, Katis NI, Frey JE. 2004. Host-associated genetic differentiation in *Thrips tabaci* (Insecta: Thysanoptera), as determined from mtDNA sequence data. *Heredity* 93:364–70

18. Brunner PC, Fleming C, Frey JE. 2002. A molecular identification key for economically important thrips species (Thysanoptera: Thripidae) using direct sequencing and a PCR-RFLP-based approach. *Agric. For. Entomol.* 4:127–36

19. Butt TM, Brownbridge M. 1997. Fungal pathogens of thrips. See Ref. 85, pp. 399–433

20. Campbell LR, Robb KL, Ullman DE. 2004. *The complete Tospovirus host list.* http://www.oznet.ksu.edu/tospovirus/host list.html

21. Carpenter A, Wright S, Lash P. 1996. Response of adult New Zealand flower thrips, *Thrips obscuratus* (Thysanoptera: Thripidae), to high carbon dioxide and low oxygen atmospheres at various temperatures. *Bull. Entomol. Res.* 86:217–21

22. Castineiras A, Peña JE, Duncan R, Osborne L. 1996. Potential of *Beauveria bassiana* and *Paecilomyces fumosoroseus* (Deuteromycotina: Hyphomycetes) as biological control agents of *Thrips palmi* (Thysanoptera: Thripidae). *Fla. Entomol.* 79:458–61

23. Childers CC. 1997. Feeding and oviposition injuries to plants. See Ref. 85, pp. 505–37

24. Childers CC, Achor DS. 1995. Thrips feeding and oviposition injuries to economic plants, subsequent damage and host responses to infestation. See Ref. 130, pp. 31–51

25. Cloutier C, Johnson SG. 1993. Interaction between life stages in a phytoseiid predator: western flower thrips prey killed by adults as food for protonymphs of *Amblyseius cucumeris*. *Exp. Appl. Acarol.* 17:441–49

26. Costa HS, Robb KL. 1999. Effects of ultraviolet-absorbing greenhouse plastic films on flight behavior of *Bemisia argentifolii* (Homoptera: Alreyrodidae) and *Frankliniella occidentalis* (Thysanoptera: Thripidae). *J. Econ. Entomol.* 92:557–62

27. Costa HS, Robb KL, Wilen CA. 2002. Field trials measuring the effects of ultraviolet-absorbing greenhouse plastic films on insect populations. *J. Econ. Entomol.* 95:113–20

28. Culbreath AK, Todd JW, Brown SL. 2003.

Epidemiology and management of tomato spotted wilt in peanut. *Annu. Rev. Phytopathol.* 41:53–75

29. De Jager CM, Butot RPT, Klinkhamer PGL, Van der Meijden E. 1995. Chemical characteristics of chrysanthemum cause resistance to *Frankliniella occidentalis* (Thysanoptera: Thripidae). *J. Econ. Entomol.* 88:1746–53

30. Eigenbrode SD, Trumble JT. 1994. Host-plant resistance to insects in integrated pest-management in vegetable crops. *J. Agric. Entomol.* 11:201–24

31. Ekesi S, Maniania NK, Ampong-Nyarko K. 1999. Effect of temperature on germination, radial growth and virulence of *Metarhizium anisopliae* and *Beauveria bassiana* on *Megalurothrips sjostedti*. *Biocontrol Sci. Tech.* 9:177–85

32. Ekesi S, Maniania NK, Onu I, Loehr B. 1998. Pathogenicity of entomopathogenic fungi (Hyphomycetes) to the legume flower thrips, *Megalurothrips sjostedti* (Trybom Thysan., Thripidae). *J. Appl. Entomol.* 122:629–34

33. Frei A, Bueno JM, Diaz-Montano J, Gu H, Cardona C, Dorn S. 2004. Tolerance as a mechanism of resistance to *Thrips palmi* in common beans. *Entomol. Exp. Appl.* 112:73–80

34. Frey JE. 1993. The analysis of arthropod pest movement through trade in ornamental plants. In *Plant Health and the European Single Market*, ed. D. Ebbels, pp. 157–65. *Br. Crop Prot. Monogr.* No. 54. Farnham, UK: Br. Crop Prot. Counc.

35. Froud KJ, Stevens PS, O'Callaghan M. 1997. Life table comparison between the parasitoid *Thripobius semiluteus* and its host greenhouse thrips. *Proc. 50th N. Z. Plant Prot. Conf.*, pp. 232–35. Canterbury, N. Z.: N. Z. Plant Prot. Soc.

36. Funderburk J, Stavisky J, Olson S. 2000. Predation of *Frankliniella occidentalis* (Thysanoptera: Thripidae) in field peppers by *Orius insidios*us (Hemiptera: Anthocoridae). *Environ. Entomol.* 29:376–82

37. Gecan JS, Bandler R, Glaze LE, Atkinson JC. 1983. Microanalytical quality of ground and unground oregano, ground cinnamon and ground nutmeg. *J. Food Prot.* 46:387–90

38. Gecan JS, Bandler R, Glaze LE, Atkinson JC. 1986. Microanalytical quality of ground and unground marjoram, sage and thyme, ground allspice, black pepper and paprika. *J. Food Prot.* 49:216–21

39. Gillespie DR. 1989. Biological control of thrips (Thysanoptera: Thripidae) on greenhouse cucumber by *Amblyseius cucumeris*. *Entomophaga* 34:185–92

40. Grafton-Cardwell EE, Ouyang Y, Bugg RL. 1999. Leguminous cover crops to enhance population development of *Euseius tularensis* (Acari: Phytoseiidae) in citrus. *Biol. Control* 16:73–80

41. Gray GM, Allen JC, Burmaster DE, Gage SH, Hammitt JK, et al. 1998. Principles for conduct of pest risk analyses: report of an expert workshop. *Risk Anal.* 18:773–80

42. Greer L, Dole JM. 2003. Aluminum foil, aluminum-painted plastic, and degradable mulches increase yields and decrease insect-vectored viral diseases of vegetables. *HortTechnology* 13:276–84

43. Grevstad FS. 1999. Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. *Biol. Inv.* 1:313–23

44. Grout TG, Richards GI. 1992. The dietary effect of windbreak pollens on longevity and fecundity of a predacious mite *Euseius addoensis addoensis* (Acari: Phytoseiidae) found in citrus orchards in South Africa. *Bull. Entomol. Res.* 82:317–20

45. Groves RL, Walgenbach JF, Moyer JW, Kennedy GG. 2002. The role of weeds and tobacco thrips, *Frankliniella fusca,* in the epidemiology of tomato spotted wilt virus. *Plant Dis.* 86:573–82

46. Hallman GJ, Schwalbe CP, eds. 2002. *Invasive Arthropods in Agriculture:*

Problems and Solutions. Enfield, NH: Sci. Publ. 450 pp.

47. Hammond DG, Rangel S, Kubo I. 2000. Volatile aldehydes are promising broad-spectrum postharvest insecticides. *J. Agric. Food Chem.* 48:4410–17

48. Hansen JD, Hara AH, Tenbrink AH. 1992. Vapor heat: a potential treatment to disinfest tropical cut flowers and foliage. *HortScience* 27:139–43

49. Hata TY, Hara AH, Jang EB, Imaino LS, Hu BKS, Tenbrink VL. 1992. Pest management before harvest and insecticidal dip after harvest as a systems approach to quarantine security for red ginger. *J. Econ. Entomol.* 85:2310–16

50. Hayase T. 1991. A list of Thysanoptera intercepted in plant quarantine. *Res. Bull. Plant Prot.* 27:93–99

51. Heger T, Trepl L. 2003. Predicting biological invasions. *Biol. Inv.* 5:313–21

52. Hochberg ME, Ives AR. 1999. Can natural enemies enforce geographical range limits? *Ecography* 22:268–76

53. Hoddle MS. 2002. Developmental and reproductive biology of *Scirtothrips perseae* (Thysanoptera: Thripidae): a new avocado pest in California. *Bull. Entomol. Res.* 92:279–85

54. Hoddle MS. 2002. Oviposition preferences of *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae) in southern California avocado orchards. *Pan-Pac. Entomol.* 78:177–83

55. Hoddle MS. 2003. Predation behaviors of *Franklinothrips orizabensis* (Thysanoptera: Aeolothripidae) towards *Scirtothrips perseae* and *Heliothrips haemorrhoidalis* (Thysanoptera: Thripidae). *Biol. Control* 27:323–28

56. Hoddle MS. 2003. The effect of prey species and environmental complexity on the functional response of *Franklinothrips orizabensis*: a test of the fractal foraging model. *Ecol. Entomol.* 28:309–18

57. Hoddle MS, Jetter KM, Morse JM. 2003. The economic impact of *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae) on California avocado production. *Crop Prot.* 22:485–93

58. Hoddle MS, Morse JG, Phillips PA, Faber BA, Jetter KM. 2002. Avocado thrips: new challenge for growers. *Calif. Agric.* 56:103–7

59. Hoddle MS, Mound LA. 2003. The genus *Scirtothrips* in Australia (Insecta, Thysanoptera, Thripidae). *Zootaxa* 268:1–40

60. Hoddle MS, Mound LA, Nakahara S. 2004. Thysanoptera recorded from California, U.S.A.: a checklist. *Fla. Entomol.* 87:317–23

61. Hoddle MS, Nakahara S, Phillips PA. 2002. Foreign exploration for *Scirtothrips perseae* Nakahara (Thysanoptera: Thripidae) and associated natural enemies on avocado (*Persea americana* Miller). *Biol. Control* 24:251–65

62. Hoddle MS, Oevering P, Phillips PA, Faber BA. 2004. Evaluation of augmentative releases of *Franklinothrips orizabensis* for control of *Scirtothrips perseae* in California avocado orchards. *Biol. Control* 30:456–65

63. Hoddle MS, Robinson L. 2004. Evaluation of factors influencing augmentative releases of *Chrysoperla carnea* for control of *Scirtothrips perseae* in California avocado orchards. *Biol. Control* 31:268–75

64. Hollingsworth RG, Sewake KT, Armstrong JW. 2002. Scouting methods for detection of thrips (Thysanoptera: Thripidae) on dendrobium orchids in Hawaii. *Environ. Entomol.* 31:523–32

65. Hood JD. 1927. A blood-sucking thrips. *Entomologist* 60:201

66. Hummel RL, Walgenbach JF, Hoyt GD, Kennedy GG. 2002. Effects of production system on vegetable arthropods and their natural enemies. *Agric. Ecosyst. Environ.* 93:165–76

67. Hurst GW. 1964. Effects of weather conditions on thrips activity. *Agric. Meteorol.* 1:130–41

68. Izzo TJ, Pinent SMJ, Mound LA. 2002. *Aulacothrips dictyotus* (Heterothripidae), the first ectoparasitic thrips (Thysanoptera). *Fla. Entomol.* 85:281–83

69. Jacobson RJ. 1997. Integrated pest management in glasshouses. See Ref. 85, pp. 639–66

70. Jacobson RJ, Chandler D, Fenlon J, Russell KM. 2001. Compatibility of *Beauveria bassiana* (Balsamo) Vuillemin with *Amblyseius cucumeris* Oudemans (Acarina: Phytoseiidae) to control *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) on cucumber plants. *Biocontrol Sci. Tech.* 11:391–400

71. Keane RM, Crawley MJ. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17:164–70

72. Kirk WDJ. 2004. The link between cereal thrips and thunderstorms. *Acta Phytopathol. Entomol. Hung.* 39:13–16

73. Kirk WDJ, Terry LI. 2003. The spread of western flower thrips *Frankliniella occidentalis* (Pergande). *Agric. For. Entomol.* 5:301–10

74. Klocke JA, Myers P. 1984. Chemical control of thrips on cultured *Simmondsia chinensis* (jojoba) shoots. *HortScience* 19:440

75. Kolar CS, Lodge DM. 2001. Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 16:199–204

76. Kowarik I. 2003. Human agency in biological invasions: Secondary releases foster naturalization and population expansion of alien plant species. *Biol. Inv.* 5:293–312

77. Kuo C, ed. 1996. *Int. Symp. Tospoviruses Thrips Floral Veg. Crops. Acta Hortic*. No. 431. 545 pp.

78. Leesch JG, Tebbets JS, Tebbets JC. 2004. Using ozone for controlling bean thrips in the navels of oranges being exported to Australia. *Proc. Int. Conf. Controlled Atmos. Fumigation Stored Prod.*, Gold Coast (AU):In press

79. Leifert C, Cassells AC. 2001. Microbial hazards in plant tissue and cell cultures. *In Vitro Cell. Dev. Biol. Plant* 37:133–38

80. Leigh TF. 1995. Bionomics of cotton thrips: a review. See Ref. 130, pp. 61–70

81. Lemelle L, Simionovici A, Susini J, Oger P, Chukalina M, et al. 2003. Imaging techniques and exobiology. *J. Physique* 204:377–80

82. Lewis T. 1964. The weather and mass flights of Thysanoptera. *Ann. Appl. Biol.* 53:165–70

83. Lewis T. 1965. The species, aerial density and sexual maturity of Thysanoptera caught in mass flights. *Ann. Appl. Biol.* 55:219–25

84. Lewis T. 1973. *Thrips: Their Biology, Ecology and Economic Importance*. London: Academic. 349 pp.

85. Lewis T, ed. 1997. *Thrips as Crop Pests*. Wallingford, UK: CABI. 349 pp.

86. Lim UT, Van Driesche RG, Heinz KM. 2001. Biological attributes of the nematode, *Thripinema nicklewoodi*, a potential biological control agent of western flower thrips. *Biol. Control* 22:300–6

87. Liu TC. 2004. Molecular identification of a plant quarantine pest (*Frankliniella occidentalis*) by one-tube nested PCR targeting ribosomal DNA internal transcribed spacer regions. *Prot. Bull.* 46:27–46

88. Loomans AJM. 2003. *Parasitoids as biological control agents of thrips pests*. PhD thesis. Wageningen Univ., Wageningen. 200 pp.

89. Loomans AJM, Murai T, Greene ID. 1997. Interactions with hymenopterous parasitoids and parasitic nematodes. See Ref. 85, pp. 355–97

90. Ludwig SW, Oetting RD. 2002. Efficacy of *Beauveria bassiana* plus insect attractants for enhanced control of *Frankliniella occidentalis* (Thysanoptera: Thripidae). *Fla. Entomol.* 85:270–72

91. Mack RN. 2000. Cultivation fosters plant naturalization by reducing environmental stochasticity. *Biol. Inv.* 2:111–22

92. Mack RN, Simberloff D, Lonsdale WM,

Evans H, Clout M, Bazzaz FA. 2000. Biotic invasions: causes, epidemiology, global consequences and control. *Ecol. Appl.* 10:689–710

93. MacLeod A, Head J, Gaunt A. 2004. An assessment of the potential economic impact of *Thrips palmi* on horticulture in England and the significance of a successful eradication campaign. *Crop Prot.* 23:601–10

94. Mankin RW, Grandhorst-Hubard J, Flanders KL, Zhang M, Crocker RL, et al. 2000. Eavesdropping on insects hidden in soil and interior structures of plants. *J. Econ. Entomol.* 93:1173–82

95. McDonald JR, Bale JS, Walters KFA. 1999. Temperature, development and establishment potential of *Thrips palmi* (Thysanoptera: Thripidae) in the United Kingdom. *Eur. J. Entomol.* 96:169–73

96. McIntyre JA, Hopper DA, Cranshaw WS. 1996. Aluminized fabric deters thrips from entering greenhouses. *Southwest. Entomol.* 21:135–40

97. McMurtry JA, Johnson HG, Newberger SJ. 1991. Imported parasite of greenhouse thrips established on California avocado. *Calif. Agric.* 45:31–32

98. Memmott J, Fowler SV, Hill RL. 1998. The effect of release size on the probability of establishment on biological control agents: gorse thrips (*Sericothrips staphylinus*) released against gorse (*Ulex europaeus*) in New Zealand. *Biocontrol Sci. Tech.* 8:103–15

99. Mollema C, Cole RA. 1996. Low aromatic amino acid concentrations in leaf proteins determine resistance to *Frankliniella occidentalis* in four vegetable crops. *Entomol. Exp. Appl.* 78:325–33

100. Moritz G, Kumm S, Mound L. 2004. Tospovirus transmission depends on thrips ontogeny. *Virus Res.* 100:143–49

101. Moritz G, Mound LA, Morris DC. 2001. *ThripsID: pest thrips of the world*. CD-ROM. Canberra, Aust.: ACIAR

102. Moritz G, Mound LA, Morris DC, Goldarazena A. 2004. *Pest thrips of the world: an identification and information system using molecular and microscopical methods*. CD-ROM. Brisbane, Aust.: Cent. Biol. Inf. Technol.

103. Morris DC, Mound LA. 2003. Thysanoptera phylogeny: the molecular future. *Entomol. Abh.* 61:153–55

104. Morris DC, Mound LA. 2004. Molecular relationships between populations of South African citrus thrips (*Scirtothrips aurantii* Faure) in South Africa and Queensland, Australia. *Aust. J. Entomol.* 43:353–58

105. Morse JG, Klonsky K. 1994. Pesticide use on California citrus: a baseline to measure progress in adoption of IPM. *Calif. Grower* 18:1619–26

106. Morse JG, Metcalf RL, Arpaia ML, Rice RE. 1995. Risks of exotic pest introductions from importation of fresh Mexican Hass avocados in the United States. *Rep. Univ. Calif. Center Exotic Pest Res.*, Riverside, Calif. 163 pp.

107. Mound LA. 1983. Natural and disrupted patterns of geographical distribution in Thysanoptera (Insecta). *J. Biogeogr.* 10:119–33

108. Mound LA. 1997. Biological diversity. See Ref. 85, pp. 197–215

109. Mound LA. 2002. So many thrips—so few tospoviruses. *Thrips and Tospoviruses: Proc. 7th Int. Symp. Thysanoptera*, pp. 15–18. Canberra: Aust. Natl. Insect Collect.

110. Mound LA. 2004. Thysanoptera: diversity and interactions. *Annu. Rev. Entomol.* 50:247–69

111. Mound LA, Kirby G. 1998. *Thysanoptera: An Identification Guide*. Wallingford, UK: CABI. 70 pp.

112. Mound LA, Marullo R. 1996. The thrips of Central and South America: an introduction (Insecta: Thysanoptera). *Mem. Entomol. Int.* 6:1–487

113. Mound LA, Marullo R, Trueman JWH. 2001. The greenhouse thrips, *Heliothrips haemorrhoidalis*, and its generic relationships within the subfamily

Panchaetothripinae (Thysanoptera: Thripidae). *Insect Syst. Evol.* 32:205–16

114. Mound LA, Ritchie S, King J. 2002. Thrips (Thysanoptera) as a public nuisance: a Queensland case study and overview, with comments on host plant specificity. *Aust. Entomol.* 29:25–28

115. Mound LA, Teulon DAJ. 1995. Thysanoptera as phytophagous opportunists. See Ref. 130, pp. 3–19

116. Mound LA, Walker AK. 1982. Terebrantia (Insecta: Thysanoptera). *Fauna N. Z.* 1:1–113

117. Mound LA, Walker AK. 1987. Thysanoptera as tropical tramps: new records from New Zealand and the Pacific. *N. Z. Entomol.* 9:70–85

118. Mound LA, Zur Strassen R. 2001. The genus *Scirtothrips* (Thysanoptera: Thripidae) in Mexico: a critique of the review by Johansen & Mojica-Guzman (1998). *Folia Entomol. Mex.* 40:133–42

119. Moy JH, Wong L. 2002. The efficacy and progress in using radiation as a quarantine treatment of tropical fruits: a case study in Hawaii. *Radiat. Physics Chem.* 63:397–401

120. National Research Council. 2000. *Incorporating Science, Economics and Sociology in Developing Sanitary and Phytosanitary Standards in International Trade*. Washington, DC: Natl. Acad. Press

121. Neuenschwander P, Markham R. 2001. Biological control in Africa and its possible effects on biodiversity. In *Evaluating Indirect Ecological Effects of Biological Control*, ed. E Wajnberg, JK Scott, PC Quimby, pp. 127–46. Wallingford, UK: CABI

122. Nickle DA. 2003. A checklist of commonly intercepted thrips (Thysanoptera) from Europe, the Mediterranean, and Africa at U.S. ports-of-entry (1983–1999). Part 1. Key to genera. *Proc. Entomol. Soc. Wash.* 105:80–99

123. Nickle DA. 2004. Commonly intercepted thrips (Thysanoptera) from Europe, the Mediterranean, and Africa at U.S. ports-

of-entry (1983–1999). Part II. *Frankliniella* Karny and *Iridothrips* Priesner (Thripidae). *Proc. Entomol. Soc. Wash.* 106:438–52

124. Norris RJ, Memmott J, Lovell DJ. 2002. The effect of rainfall on the survivorship of a biocontrol agent. *J. Appl. Ecol.* 39:226–34

125. Ohta I. 2002. Host plant resistance in Japanese chrysanthemums against *Frankliniella occidentalis* (Thysanoptera: Thripidae) during the non-flowering stage. *Appl. Entomol. Zool.* 37:271–77

126. Omer AD, Granett J, Karban R, Villa EM. 2001. Chemically-induced resistance against multiple pests in cotton. *Int. J. Pest Manag.* 47:49–54

127. Palmer JM, Mound LA, du Heaume GJ. 1989. *IIE Guides to Insects of Importance to Man.* No. 2: *Thysanoptera*. Wallingford, UK: CABI. 73 pp.

128. Palmer WA. 2005. Corrections to Morris and Mound (2004) 'Molecular relationships between populations of South African citrus thrips (*Scirtothrips aurantii* Faure) in South Africa and Queensland, Australia.' *Aust. J. Entomol.* 44:1

129. Parker BL, Skinner M. 1997. Integrated pest management (IPM) in tree crops. See Ref. 85, pp. 615–38

130. Parker BL, Skinner M, Lewis T. 1995. *Thrips Biology and Management*. New York: Plenum. 636 pp.

131. Parrella G, Gognalons P, Gebre-Selassie K, Vovlas C, Marchoux G. 2003. An update on the host range of tomato spotted wilt virus. *J. Plant Pathol.* 85:227–64

132. Parrella MP, Lewis T. 1997. Integrated pest management (IPM) in field crops. See Ref. 85, pp. 594–614

133. Perez-Mendoza J, Throne JE, Dowell FE, Baker JE. 2003. Detection of insect fragments in wheat flower by near-infrared spectroscopy. *J. Stored Prod. Res.* 39:305–12

134. Peters D, Wijkamp I, Van de Wetering F, Goldbach R. 1995. Vector relations

in the transmission and epidemiology of tospoviruses. See Ref. 77, pp. 29–43

135. Potter MA, Carpenter A, Stocker A, Wright S. 1994. Controlled atmospheres for the postharvest disinfestation of *Thrips obscuratus* (Thysanoptera, Thripidae). *J. Econ. Entomol.* 87:1251–55

136. Premachandra WTSD, Borgemeister C. 2003. Combined releases of entomopathogenic nematodes and the predatory mite *Hypoaspis aculeifer* to control soil-dwelling stages of western flower thrips *Frankliniella occidentalis*. *Biocontrol* 48: 529–41

137. Reboredo M, De Morentin IM, Moriyon I, Jordana R. 2003. A methodology for thrips larvae identification using protein profiles obtained by SDS-PAGE. *BioControl* 48:295–406

138. Reitz SR, Yearby EL, Funderburk JE, Statisky J, Momol MT, Olson SM. 2003. Integrated management tactics for *Frankliniella* thrips (Thysanoptera: Thripidae) in field-grown peppers. *J. Econ. Entomol.* 96:1201–14

139. Shea K, Chesson P. 2002. Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17:170–76

140. Shelton AM, Nault BA, Plate J, Zhao J-Z. 2003. Regional and temporal variation in susceptibility to lamba–cyhalothrin in onion thrips, *Thrips tabaci* (Thysanoptera: Thripidae), in onion fields in New York. *J. Econ. Entomol.* 96: 1843–48

141. Shelton AM, Wilsey WT, Schmaedick MA. 1998. Management of onion thrips (Thysanoptera: Thripidae) on cabbage by using plant resistance and insecticides. *J. Econ. Entomol.* 91:329–33

142. Shibao M. 1996. Effects of a vinyl film cover on the population density of the chillie thrips, *Scirtothrips dorsalis* Hood (Thysanoptera: Thripidae), on grape. *Appl. Entomol. Zool.* 31:174–77

143. Shipp JL, Wang K. 2003. Evaluation of *Amblyseius cucumeris* (Acari: Phytoseiidae) and *Orius insidiosus* (Hemiptera: Anthocoridae) for control of *Frankliniella occidentalis* (Thysanoptera: Thripidae) on greenhouse tomatoes. *Biol. Control* 28:271–81

144. Smith JF. 2003. International trade agreements and sanitary and phytosanitary measures. See Ref. 146, pp. 39–54

145. Sumner DA. 2003. Economics of policy for exotic pests and diseases: principles and issues. See Ref. 146, pp. 9–18

146. Sumner DA, ed. 2003. *Exotic Pests and Diseases: Biology and Economics for Biosecurity*. Ames, IA: Blackwell. 265 pp.

147. Throne JE, Hallman GJ, Johnson JA, Follett PA. 2003. Post-harvest entomology research in the United States Department of Agriculture—Agricultural Research Service. *Pest Manag. Sci.* 59:619–28

148. Toda S, Komazaki S. 2002. Identification of thrips species (Thysanoptera: Thripidae) on Japanese fruit trees by polymerase chain reaction and restriction fragment length polymorphism of the ribosomal ITS2 region. *Bull. Entomol. Res.* 92:359–63

149. Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM. 2003. Introduced species and their missing parasites. *Nature* 421:628–30

150. Trichilo PJ, Leigh TF. 1986. Predation on spider mite eggs by the western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), an opportunist in a cotton agroecosystem. *Ecol. Entomol.* 15:821–25

151. Ullman DE, Meideros R, Campbell LR, Whitfield AE, Sherwood JL, German TL. 2002. Thrips as vectors of tospoviruses. *Adv. Bot. Res.* 36:113–40

152. Ullman DE, Sherwood JL, German TL. 1997. Thrips as vectors of plant pathogens. See Ref. 85, pp. 539–65

153. USDA. 2004. Treatment manual. U.S.

Dep. Agric. APHIS-PPQ. Updated 9-17-04. http://www.aphis.usda.gov/ppq/manuals/pdf_files/Treatment_Chapters.htm

154. Vail PV. 2001. Postharvest management of bean thrips. In *2000 Annual Report, Citrus Research Board*, p. 58. Visalia, CA: Citrus Res. Board

155. Van de Klashorst G, Tamo M. 1995. Ecologically sustainable management of bean thrips in Africa. See Ref. 130, pp. 393–96

156. VanvHalteren P. 1995. A diagnostic network for the EPPO region. *EPPO Bull.* 25:1–4

157. Van Houten YJ, Van Rijn PCJ, Tanigoshi LK, Van Stratum P, Bruin J. 1995. Preselection of predatory mites to improve year-round biological control of western flower thrips in greenhouse crops. *Entomol. Exp. Appl.* 74:225–34

158. Van Rijn PCJ, Mollema C, Steenhuis-Broers GM. 1995. Comparative life history studies of *Frankliniella occidentalis* and *Thrips tabaci* (Thysanoptera: Thripidae) on cucumber. *Bull. Entomol. Res.* 85:285–97

159. Vierbergen G. 1995. International movement, detection, and quarantine of Thysanoptera pests. See Ref. 130, pp. 119–32

160. Vierbergen G. 1996. After introduction of *Frankliniella occidentalis* in Europe: prevention of establishment of *Thrips palmi* (Thysanoptera: Thripidae). *Acta Phytopathol. Entomol. Hung.* 31:267–72

161. Waggoner M, Ohr HD, Adams C, Sims JJ, Gonzalez D. 2000. Methyl iodide an alternative to methyl bromide for insectary fumigation. *J. Appl. Entomol.* 124:113–17

162. Warnock DF. 2003. Resistance to western

flower thrips feeding damage in *Impatiens* populations from Costa Rica. *HortScience* 38:1424–27

163. Whitfield AE, Ullman DE, German TL. 2005. Tospovirus-thrips interactions. *Annu. Rev. Phytopathol.* 43:In press

164. Williams CB. 1921. A blood-sucking thrips. *Entomologist* 54:163–64

165. Worner SP. 2002. Predicting the invasion potential of exotic insects. See Ref. 46, pp. 119–37

166. Wysoki M, Kuzlitzky W, Izhar Y, Swirski E, Ben-Yehuda S, et al. 1997. Successful acclimatization of *Thripobius semiluteus*, a parasitoid of *Heliothrips haemorrhoidalis* (Bouche) in Israel. *Phytoparasitica* 25:155

167. Yano E, Matsuo K, Shiyomi M, Andow DA, eds. 1997. *Biological Invasions of Ecosystem by Pests and Beneficial Organisms*. Ser. 3. Tsukuba, Jpn: NIAES. 232 pp.

168. Yencho GC, Cohen MB, Byrne PF. 2000. Applications of tagging and mapping insect resistance loci in plants. *Annu. Rev. Entomol.* 45:393–422

169. Yokoyama VY, Miller GT. 2000. Response of omnivorous leafroller (Lepidoptera: Tortricidae) and onion thrips (Thysanoptera: Thripidae) to low-temperature storage. *J. Econ. Entomol.* 93: 1031–34

170. Yokoyama VY, Miller GT, Crisosto CH. 2001. Pest response in packed table grapes to low temperature storage combined with slow-release sulfur dioxide pads in basic and large-scale tests. *J. Econ. Entomol.* 94:984–88