INVASION BIOLOGY OF THRIPS

Joseph G. Morse and Mark S. Hoddle

Department of Entomology, University of California, Riverside, California 92521; email: joseph.morse@ucr.edu, mark.hoddle@ucr.edu

Key Words  Thysanoptera, opportunists, invasive species, tospoviruses

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 thrips, 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 Phlaothripidae can induce leaf galls (e.g., *Gynaikothrips ficorum*). The impressive *Idolothrips spectrum* (Phlaothripidae) 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 *Hercothrips femoralis* and *Chaetanaphothrips 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 occidentalis*, *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 appearance, 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 human 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 reductions in crop yield. On 12 selected field crops, feeding by Thysanoptera resulted 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 *Chaetanaphthrips 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.
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 fewer 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 (11). 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 website at [https://www.ippc.int/IPP/En/default.jsp](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-APHIS 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. auranti* 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 chemical 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 successful. 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 period, 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, relaxation 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 straightjacketed 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.

ACKNOWLEDGMENTS

We thank Drs. Carl Childers, Timothy Grout, Michael Parrella, Laurence Mound, Gerald Moritz, and Anthony Shelton for reviewing earlier drafts of this manuscript, and Lindsay Robinson for assistance with literature searches. Comments by two anonymous reviewers were also useful.

The Annual Review of Entomology is online at http://ento.annualreviews.org

LITERATURE CITED

8. Baker RHA. 2002. Predicting the limits to the potential distribution of alien crop pests. See Ref. 46, pp. 207–41
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
Epidemiology and management of tomato spotted wilt in peanut. *Annu. Rev. Phytopathol.* 41:53–75


Morse • Hoddle


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


92. Mack RN, Simberloff D, Lonsdale WM,


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


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


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


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


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