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Invasion Biology, Ecology, and Management of Western Flower Thrips

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Abstract

The western flower thrips, *Frankliniella occidentalis*, first arose as an important invasive pest of many crops during the 1970s-1980s. The tremendous growth in international agricultural trade that developed then fostered the invasiveness of western flower thrips. We examine current knowledge regarding the biology of western flower thrips, with an emphasis on characteristics that contribute to its invasiveness and pest status. Efforts to control this pest and the tospoviruses that it vectors with intensive insecticide applications have been unsuccessful, and have created significant problems because of the development of resistance to numerous insecticides and associated outbreaks of secondary pests. We synthesize information on effective integrated management approaches for western flower thrips that have developed through research on its biology, behavior and ecology. We further highlight emerging topics regarding the species status of western flower thrips, as well as its genetics, biology, and ecology that facilitate its use as a model study organism and will guide development of appropriate management practices.

Keywords

Invasive alien species, cryptic species, Integrated pest management (IPM), *Tospovirus,* genomics, Thysanoptera

Western Flower Thrips Importance and Biology

Western flower thrips (WFT), *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), first arose as one of the world's most important, invasive pests of horticultural and agronomic crops during the 1970s-1980s (100). Economic damage results directly through feeding and oviposition, and indirectly through transmission of plant pathogenic viruses in the genus *Tospovirus* (Peribunyaviridae) (64). WFT-induced crop injury results in quantitative yield losses and reduction in quality. Because of difficulties in managing WFT, losses can be especially severe for high-value produce and ornamental crops where aesthetic damage is unacceptable, and for quarantine interdictions (16). Reliable estimates of economic losses are scarce and difficult to determine. However, given the broad host range of WFT and the plant pathogenic viruses it transmits, economic losses are likely very large (e.g., 41).

Before the invasive outbreaks that began in the 1970s, WFT was a sporadic pest in its native range of western North America (6, 13), with one of the earliest accounts of its pest status being published in 1915 (23). The earliest record of WFT as an adventive species is based on populations infesting tree lupin (*Lupinus arboeus*) in New Zealand (83). Yet those populations have not become invasive, agricultural pests as have more recently introduced populations (68). The recent worldwide growth in the commercial movement of plant materials has allowed for a rapid expansion of WFT's range throughout North America, South America, Australia, Oceania, Africa, Europe, and Asia (15). Even in areas where WFT has long been established, it is becoming more prevalent and damaging (11, 36).

Concomitant with this spreading and growing threat, research on WFT biology, ecology, and management has increased in recent years. Since Reitz (100) summarized the number of scientific publications on WFT in 2009, more than 1,000 articles concerning WFT have been published. While this ongoing research has shed much light on the complex life history of WFT and its pest status, many new questions regarding this species have arisen.

The intense research resulting from its pest status offers a foundation for WFT as a model organism for the study of multitrophic interactions. WFT preys on eggs and immatures of other arthropods, including pests such as spider mites, and therefore it may serve as a biological control agent (135). Predation provides extra dietary protein, which increases WFT reproductive success (138). The association appears to be more than a facultative relationship, with WFT attracted to spider mite infestations (70). WFT feeding also can be detrimental to other herbivorous pest insects through plant-mediated effects (95).

A species complex?

One of the great challenges in understanding WFT is determining whether it comprises a single species or a cryptic species complex. As discussed above, the existence of a non-pest strain inhabiting lupin in New Zealand has been known since the 1930s. Rugman-Jones et al (109) identified two genetically distinct, reproductively isolated biotypes with overlapping distributions in the putative native range of California. Although they designated WFT as two species, terming one as the “Glasshouse” and the other as the “Lupin” species because of its correspondence with the New Zealand lupin population, no formal taxonomic, biological, or behavioral studies have been undertaken to confirm that these two molecularly separable entities are distinct species.

Circumstantial evidence points to the Glasshouse type as being a much greater pest than the Lupin type (10, 68). It is unknown, and may never be ascertained, if variation observed in results among similar studies is from interpopulation variation of a highly polymorphic species, or from the studies being conducted with different species, or with mixtures of species (109).

A survey in the Netherlands determined all specimens to be the Glasshouse strain (74). Interestingly, these populations varied in their performance, with the highest reproduction of each occurring on their natal host. In contrast, the recent invasion of China involves both the Glasshouse and Lupin types, yet with the Glasshouse type being predominant (30). Ongoing surveys in China are proving useful in revealing the invasion process, and may aid in providing tailored management options for the particular type or types present in a region. Surveyed populations had similar haplotypes but low interpopulation gene flow, suggesting human activities facilitate WFT movement and that the invasion process has been the result of multiple introductions (16).

WFT demonstrates strong host plant affinities in other invaded regions, which has pest management implications. Kenyan populations, which are comprised of the Glasshouse strain (62), show greater genetic differentiation among host plant species than among regions, which suggests reduced gene flow among hosts and the possible development, or existence, of biotypes (48).

Another phylogeographic study identified two genetically distinct ecotypes of *F. occidentalis* in western North America (12). These ecotypes segregate by habitat. One is associated with cool/moist habitats, and the other is associated with hot/dry habitats. Populations that are widely separated spatially but come from similar habitats are more closely related than are populations that are geographically close but from different habitats. Despite these differences, the authors did not consider the genetic differentiation between the types to be great enough to justify the designation of two species. It is also not clear how the cool/moist ecotype and hot/dry ecotype may relate to the Glasshouse and Lupin types. Given the uncertain taxonomic status of WFT, we use a broad interpretation of *F. occidentalis* to accommodate all known biotypes through the remainder of our review but reiterate the need for a thorough taxonomic accounting of *F. occidentalis*.

Life Cycle and Reproduction

WFT exhibits arrhenotokous reproduction, with females arising from fertilized eggs and males from unfertilized eggs. However, virgin females occasionally produce female offspring (thelytoky) (58). Sex ratios of progeny from mated females are female-biased (46), yet females do not appear to allocate the sex of their offspring (131). Therefore, variations in sex ratios among populations likely result from differences between the sexes in dispersal, within plant distribution, and longevity.

Eggs are deposited within plant material, often under the epidermis of leaves. Larvae pass through two feeding instars, before entering the non-feeding and relatively immobile propupal and pupal stages (13). Pupae drop from host plants to complete pupation in the soil. Host plant abandonment is influenced by ambient conditions, such as time of day (47), relative humidity (125), or structural complexity of the host plant (14). Winged adults emerge from the pupal stage. Development is temperature dependent with temperatures needing to be above a minimum of 8-10^{o}C for growth, and optimal developmental rates occurring between 25-30^{o}C (100). Developmental rates also are influenced by photoperiod, with slower growth occurring under shorter day lengths (9). Despite its presence throughout montane regions of western North America (13), cold hardiness studies indicate that WFT has a supercooling point of -26°C and prolonged exposure to subfreezing temperatures is lethal (136). Therefore, adults may only overwinter in areas with mild winters or where adequate shelter from prolonged extreme cold exists. Cold exposure also reduces fitness of surviving females (72). Adult exposure to heat (>41^{o}C) reduces production of offspring and proportions of female offspring, and the survivorship of those progeny (140). Under optimal laboratory conditions, adults may live 2-5 weeks, but longevity is likely shorter in the field (100).

Behavior and Dispersal

Flight and dispersal

As relatively small insects, WFT are weak flyers that rely on dispersal by wind for long distance transport (81). At small spatial scales, WFT show directed flight to host cues, which result in differential host plant distributions (133), and to conspecifics (54). Mark-recapture studies in greenhouses indicate that adult WFT disperse very short distances from release points (< 0.3 m/day) (102) with similar short-range movement occurring in open fields (88). Flight is diurnal, and is affected by temperature and wind speed (97).

Pheromones

WFT has complex pheromone biology. Adult males produce an aggregation pheromone that attracts both sexes. Its effect is amplified in the presence of appropriate visual cues (54). This pheromone influences interactions among males and between the sexes (55), including male aggregations where male-male combat and mating occur (130). Another male-produced contact pheromone possibly functions as a substrate marker that delineates “territory” for male-male fighting and mating (94). Larvae produce an alarm pheromone that is released in anal secretions. However, effects are weak, which limits the potential for pest management (127). In contrast, the greater range of attraction for the aggregation pheromone increases its utility for pest monitoring and management (54). One avenue with potential to improve management is through using the aggregation pheromone for mass trapping (112).

Host Location and Selection

Directed movement toward hosts and final selection are driven by different visual, morphological and chemical cues and the interaction among those cues (18, 66). In terms of color, light in the yellow and ultraviolet (UV) range has the greatest effects on host plant selection (108). UV-light reflectance can be manipulated for management. UV-absorbing films and nets interfere with thrips dispersal, orientation, and host-finding, and consequently, reduce infestations of crops in protected culture (52). Likewise, UV-reflective mulches disrupt host location and significantly reduce populations in open field crops (101).

In addition to color, WFT use shape as a host location cue. Circular shapes are more attractive than other simple geometric shapes, but WFT spend more time on complex "floral" shapes than on simpler geometric patterns (66). In terms of complex shapes, WFT prefer rounded floral patterns to more irregular patterns.

WFT also use different plant volatiles as part of their host location repertoire (18, 66). Given the tremendous polyphagy of the species, it is not surprising that a wide range of plant-related volatiles affect WFT behavior, including phenylpropanoids, monoterpenes, sesquiterpenes, esters, and 4-pyridyl carbonyl compounds (26, 56). Methyl isonicotinate is particularly effective as an attractant for trapping although it is not particularly widespread in plants (132). It may generate a response because of its structural similarity to other floral volatiles (26). Chemoreception in WFT is plastic. Zhang and Lei (148) identified a chemosensory protein in WFT antennae with binding affinities to various plant volatiles, including anisic aldehyde, geraniol, and methyl salicylate.

In addition to interactions among plant cues, host location and selection are influenced by the physiological state of the thrips. Adult responses to external cues are affected by sex, age, levels of satiation (24), and motivation to oviposit (18). Certain volatiles and colors that are attractive to females elicit no response in males. These results suggest that discrimination among potential host plants is driven to a large extent by oviposition choices. In contrast to the wide range of attractants, few volatile repellents have been identified, although certain attractants become repellent at high concentrations (56). Further, induction of plant volatiles by other herbivores can reduce WFT attraction to host plants (28).

Feeding and oviposition

Upon landing, adults examine a potential host for appropriate chemical and physical cues for feeding by moving antennae and labial sensilla over the surface. Final acceptance of a host plant after landing is dependent on the nutritional quality of the food source relative to its defensive compounds. For example, WFT prefer cultivated tomato (*Solanum lycopersicum*) to wild types. This difference could be linked to the wild types having higher levels of acylsugars, which are feeding and oviposition deterrents (73). WFT avoid younger leaves of *Senecio* spp., which are better defended by greater concentrations of toxic pyrrolizidine alkaloids than are older leaves (59). On thrips-resistant cultivars of cucumber (*Cucumis sativus*), WFT spend more time walking to widely dispersed feeding sites than on susceptible cultivars in which suitable feeding sites are more densely clumped.

When stimuli indicate a plant is an appropriate food source, probing is initiated. Electronic monitoring has revealed different modes of feeding: non-ingestion probes, frequent short ingestion probes, which last only a few seconds, and less frequent long ingestion probes, which may last over an hour (53). Females feed more intensively than males, which is attributed to their lower mobility and high consumption rates needed for egg production (93). However, most feeding studies have concentrated on second instars and adults, which are of similar size. First instars are much smaller and may be unable to probe as deep and extensively as older stages (120).

The piercing-sucking mouthparts of WFT provide an exceptional feeding mechanism (50). The single mandibular stylet pierces the wall of epidermal cells. Because the mandible is fused to the exoskeleton, it cannot be protracted. Instead, the entire head moves downwards and backwards. Subsequent to cell rupture, the maxillary stylets, which interlock to form a feeding tube, are inserted to macerate tissues, and saliva is secreted (121). WFT are able to feed on epidermal, palisade and spongy mesophyll cells.

Based on genes encoding for WFT salivary proteins, saliva is instrumental in the digestion of complex sugars and proteins, and is involved in extra-oral digestion of cell wall components and contents (121). In addition, thrips saliva activates genes implicated in counteracting plant defense responses.

Because adults and larvae feed in a similar manner, both stages contribute to plant damage. An individual feeds on multiple cells during a single probe (53). Prolonged thrips feeding results in extensive pockets of cell damage in which only remnants of cell walls and organelles remain (53). Variation in the depth and extent of feeding is reflected in the time spent at each feeding hole, ranging from a few seconds to more than an hour.

Based on reciprocal feeding and oviposition experiments, WFT collected from different crops show little difference in amounts of feeding across tested hosts (74). However, reproductive success is highest on their original host. Rahman et al (99) reported that the preferred strawberry (*Fragaria × ananassa*) cultivar for adult feeding is also the most suitable one for reproduction. The correlation between oviposition preference and larval performance indicate that populations can adapt to and specialize on particular hosts (17).

Because of its dietary protein content, pollen availability is important for host selection and oviposition. Adults preferentially land on flowering chrysanthemum as opposed to nonflowering ones, and they have greater reproductive success when plants are in flower (27). Female abundance increases with increasing nitrogen fertilization in both tomato and capsicum (*Capsicum annuum*). This response to nitrogen has been linked in particular to concentrations of aromatic amino acids in flowers (8). Independent of fertilization, larval feeding damage has been correlated with aromatic amino acid concentrations in different crops, indicating that WFT respond not just to total nitrogen content but to the particular forms present (75).

It is important to distinguish plant species that are hosts in which WFT successfully breed from non-host species in which flowers serve other functions, including being mating or adult feeding resources. A broad range of host and non-host species are utilized throughout agroecosystems, with adults able to distinguish among plant species suitable for oviposition, feeding, or other purposes (104). The mobile adults may be attracted to and reach high numbers in flowers of species that are not suitable reproductive hosts (82). Reproductive hosts serve as bridges to build populations that can disperse into cropping systems (87).

Crop Pest Interactions

Damage by feeding, oviposition, and virus transmission

A key factor in the importance of WFT as a pest is its polyphagy. It has been recorded feeding on over 250 crop species from over 60 families (61), yet its full host range is likely much broader. It is a pest of virtually all types of crops, including fruiting and leafy vegetables, ornamentals, tree and berry fruits, and cotton (100). In addition, WFT occurs on many uncultivated plants (87).

In addition to feeding and oviposition damage, WFT is the most efficient vector of seven species of *Tospovirus*, including Alstroemeria necrotic streak virus[1], Chrysanthemum stem necrosis tospovirus[1], *Groundnut ringspot tospovirus, Impatiens necrotic spot tospovirus, Tomato chlorotic spot tospovirus, Tomato spotted wilt tospovirus* (TSWV), and Tomato zonate spot virus[1] (107).

Feeding on actively growing tissues leads to stunting and distorted plant growth, with eventual yield loss (141). As plant cells are drained of contents, they become filled with air, leading to silvered foliage characteristic of heavily injured plants. Feeding on flower buds inhibits growth, resulting in small or deformed flowers, streaking and discoloration of floral petals (20). Feeding on immature fruits and vegetables results in scarring and russetting as fruits develop (99, 141). Collectively, feeding injury reduces the aesthetic value and storage quality of produce (20).

In addition, feeding predisposes plant tissue to subsequent invasion by bacterial or fungal pathogens, as shown for *Fusarium* ear rot in corn (35). Table grapes fed upon by WFT tend to split during ripening, which leads to subsequent rot (43). Black fecal droplets provide media for

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[1] Alstroemeria necrotic streak tospovirus, Chrysanthemum stem necrosis tospovirus and Tomato zonate spot tospovirus are proposed species

fungi to grow on plant surfaces (20). A different form of injury is inflicted by WFT entering unopened flower buds to feed on pollen, which may interfere with pollination (111).

Plant responses to feeding injury and virus infection

WFT feeding induces jasmonic acid (JA) signalling, required for the onset of plant defenses, which in turn affect WFT responses to these potential hosts (124). The majority of genes expressed in *Arabidopsis* upon WFT feeding are JA-responsive, leading to increased JA concentrations (2). WFT show lower preference for tomato plants in which JA-defenses have been activated through thrips feeding. This defense response leads to increases in densities of leaf glandular trichomes and production of volatiles (32).

In contrast to the expression of plants infested just with WFT, TSWV-infected *Arabidopsis* increases expression of salicylic acid (SA)-regulated genes and reduce expression of JA-responsive ones (3). Enhanced preference and performance of WFT on virus-infected plants (67, 91, 118) appear to be regulated by antagonistic plant defenses, whereby SA-regulated plant defenses induced by virus infection suppress JA-regulated plant defenses against WFT.

Interactions with Tospovirus Species

Worldwide, WFT is the most important vector of tospoviruses, including TSWV which is the most economically important species (115). WFT become competent tospovirus vectors only if they acquire the virus as first or early second instars (86). However, the mechanisms that govern virus acquisition remain uncertain. The virus circulates in the haemolymph and replicates within tissues, passing from the midgut to the salivary glands (77). Specific surface receptor proteins (92) and viral glycoproteins (142) are involved in virus recognition by WFT cells. A nearly universal down-regulation of virus-responsive transcript sequences in first instars has been proposed as the reason newly eclosed larvae are the most efficient stage for virus acquisition (114). Yet, this hypothesis needs to be reconciled with a morphological hypothesis that posits viral passage to the salivary glands is limited to the brief time during the early larval phase when the midgut, visceral muscles and salivary glands are in contact (78).

Transmission of tospoviruses occurs in a persistent and propagative manner (105). Vector competence is a heritable trait (89), and consequently transmission ability varies among individuals. The ability of individuals to transmit is not constant throughout their lifetime. Transmission efficiency is related to virus titre (106), and transmission frequency is greatest in early in adulthood (71). Males, because of their less intense feeding, which is less likely to result in plant cell death, are more effective at transmission than are females (93). Viral infection further accentuates the less intense feeding behavior of males. Infected males make more noningestion probes, which cause minimal damage to plants cells and thus facilitate viral infection (123).

Although it should be adaptive for TSWV to manipulate its vectors to promote viral spread, studies of the effects of TSWV infection on WFT have yielded inconsistent support for that hypothesis. Effects on thrips may be direct through the modification of vectors by the virus or indirectly through viral modification of host plants. Exposure to TSWV-infected hosts led to shorter WFT development time in some experiments (67, 118) but had no effect in others (144). Adults reared as larvae on infected plant material tend to have lower reproductive success than adults not exposed to TSWV as larvae (91, 118, but see 150). However, reproductive success of TSWV-exposed larvae is higher when they are provisioned with uninfected plant material as adults. Infected adults are preferentially attracted to uninfected plants, whereas uninfected adults are preferentially attracted to infected plants (67, 118). Tomato infected with a non-thrips-transmissible isolate of TSWV attracts WFT (134), suggesting that attraction is mainly governed by plant-vector interactions rather than by vector-virus interactions. Virus infected plants differ from non-infected ones in appearance and nutrient contents, which may increase WFT preference. Yellowed leaves of TSWV infected plants may increase thrips attraction (118), or they may be preferred due to increased levels of free amino acids (85).

While differences among thrips populations and virus strains undoubtedly exist, studies often have not considered the interactions among thrips, virus, and host plants. It also is not reasonable to think that all modifications in vector behavior and biology are adaptive for the virus. Infected female WFT actually increase their predatory activity, perhaps to overcome deleterious effects of infection by TSWV (122). This behavioral modification may reduce virus transmission but could increase the reproductive success of virus-infected thrips.

Because tospoviruses can only be acquired by larval thrips, these viruses only propagate when the virus and its vector reproduce on the same plant. Primary spread of the virus into a crop is due to infections caused by viruliferous adults dispersing into fields from outside sources but does not require vector reproduction in the crop (63). Viruliferous adults that acquire the virus as larvae feeding in the crop cause secondary spread within the crop. Epidemics of TSWV in the field may only have one infection cycle (monocyclic) or several (polycyclic). For example, polycyclic epidemics occur when WFT reproduce in an infected crop and their resulting offspring spread virus from infected plants within the field (110). Monocyclic spread may be a function of the host being biologically unsuitable for the vector or pest management practices that limit vector reproduction resulting in a monotonic spread of virus in the crop from immigrating vectors (76).

In addition to interactions with viruses, recent research has shown that WFT has intimate associations with bacterial endosymbionts. Two endosymbionts identified to date, BFo1 and BFo2, share relationships with WFT although their effects on WFT life history are unknown (34). Genetic analyses show that BFo1 aligns with the genus *Erwinia* and BFo2 most closely aligns with the genus *Pantoea*. Although both bacterial genera contain plant pathogenic species, there is no evidence that either BFo endosymbiont is virulent.

Management

The history of WFT has shown that reliance on a single management tactic, especially a reliance on insecticides, is not an effective nor sustainable approach (40, 100). Effective management programs integrate diverse tactics, and the tactics themselves often affect WFT populations in multiple, interacting ways. While these interactions confound a simple categorization of approaches, they are critical to successful management.

Detection and Monitoring

The attraction of WFT adults to low UV-reflecting whites, yellows, and blues is exploited widely for monitoring populations (129). In particular, colored cards coated with adhesive are used for monitoring WFT. The addition of the male-produced aggregation pheromone to traps increases captures (11) and can be effective for successful mass-trapping (112). Likewise, attractive plant-derived semiochemicals can significantly enhance trap captures in protected and outdoor crops (132), and these can also attract WFT predators for improved biocontrol (25).

Trapping is valuable for monitoring the presence of adults, especially at low levels, but trapping data does not reflect population levels on the plant. Techniques to estimate relative densities of adults and larvae infesting plant material include liquid washing, mechanical dislodgement, and desiccation. However, the positive thigmotaxis, small size, and high levels of aggregation of WFT interfere with the accuracy and precision of any sampling method (126). Shipp and Zariffa (119) compared sampling methods for WFT in flowers of capsicum and found collection of blossoms to be the most cost-effective. Where mixed species populations occur, population assessments are limited by difficulties in distinguishing WFT from morphologically similar species that are not pests (29, 37). Given the different costs and benefits of sampling methods, researchers and growers should select a sampling program based on their needs and resources (126).

Economic Thresholds

Understanding pest-crop damage relationships is essential for decision-making in management of WFT (36, 112, 117). Economic thresholds are critical for effective and sustainable management, in part by avoiding unnecessary insecticide applications and conserving natural enemies (7). Economic thresholds have been established for certain fruiting vegetables to determine the short-term need to apply insecticides and the long-term need to employ preventive tactics over multiple growing seasons (29). Such economic thresholds have successfully reduced insecticide use, and allowed the incorporation of conservation biological control and other sustainable tactics, but thresholds are not yet available for all crops. Where tospovirus transmission is an overriding concern, economic thresholds are difficult to establish, but development should focus on thresholds for larvae to reduce secondary viral spread (29, 76).

Environmental conditions complicate the use of economic thresholds. For example, economic thresholds have been unsuccessful in optimizing the use of early season insecticides in cotton (22). Cotton seedlings with vigorous plant growth sustain little damage even at high thrips densities. However, plants already stressed from other causes are vulnerable to delayed fruit set if thrips injury occurs, which may confound management decisions (4). Consequently, prophylactic treatment of seeds with neonicotinoids has continued to increase, with more than 90% of cotton in the southern USA receiving seed-treatments for thrips management (4).

Host Plant Resistance

Host plant resistance as a management tactic is expressed either through resistance to thrips feeding or through resistance to thrips-transmitted viruses. Historically, resistance to thrips feeding has received less attention than has resistance to tospoviruses although this has recently begun to change. Success with either approach has been limited from cultivars being commercially unacceptable or because of outbreaks of resistance-breaking virus strains (128).

Commercial tomato cultivars that contain the dominant *Sw-5* gene confer resistance to certain thrips-transmitted tospoviruses (29). However, *Sw-5* resistance or the analogous *Tsw* hypersensitive resistance in capsicum have not proven durable because of resistance-breaking strains (128). Where resistance-breaking strains of tospoviruses emerge, additional management tactics are required (96). Suppressing WFT infestations during bloom helps to reduce inoculation pressure and disease incidence, even with TSWV-resistant cultivars (49).

Along with constitutive host plant resistance, induced defenses may be exploited for management (124). Primary plant metabolites play a central role in the nutritional ecology of WFT. Consequently, manipulating dietary nitrogen by varying soil fertility reduces preference and performance of WFT, and disease incidence from tospoviruses (8, 29). Larval development is inhibited by certain secondary metabolites (65), which may be exploited for management. An ecometabolic approach comparing metabolomic profiles of resistant and susceptible plants identified compounds that inhibit feeding by adult WFT. Metabolites involved include pyrrolizidine alkaloids, acyl-sugars, and phenylpropanoids (59, 60, 73). In addition to activation by thrips feeding, JA-mediated plant defenses in tomato that reduce thrips feeding are activated through application of ultraviolet radiation (31), high light intensity (33) or bacterial infection (19). Induced plant resistance through the application of acibenzolar-*S*-methyl, a functional analog of SA, can be an important component in the integrated management of tospoviruses (76). However, increased levels of SA can reduce JA-mediated defenses against WFT, in effect making plants more susceptible to WFT (3).

Transgenic plants that provide resistance to WFT have been developed, yet these are not in commercial use. Some transgenic cultivars express protease inhibitors that reduce the availability of amino acids for WFT growth and development, and their ability to transmit tospoviruses is also reduced (80). Transgenic cotton containing a novel *Bacillus thuringiensis* toxin protects seedlings from thrips injury (42).

Cultural Control

Cultural tactics are important components of integrated pest management programs for WFT and are among the most sustainable practices (29). These tactics include repelling adults, adversely affecting female reproductive behavior, barriers to prevent adult incursions, and recruiting natural enemies and competitor species of thrips (29, 69).

Cultural tactics are the basis of push-pull systems for WFT management. Tactics that repel (push) adult WFT from crops, such as UV-reflective mulches and fertility management, act additively or synergistically with other measures to reduce WFT densities and incidence of tospovirus infections (69). Companion plants attract (pull) adults from crops and provide floral resources for key natural enemies (e.g., *Orius* spp.) and interspecific competitors (e.g., *Frankliniella bispinosa* or *F. tritici*) (38). Collectively, cultural controls can reduce primary cycles of tospovirus disease by reducing WFT colonization of crops and secondary cycles by increasing natural enemy and competitor species abundance in the crop (137).

Biological Control

Of the numerous species of natural enemies that attack WFT, anthocorid bugs are among the most important as biological control agents in open field and protected-culture crops. Species in the genus *Orius* suppress populations of WFT on crop and non-crop plants (38, 80). Conserving anthocorids is the most important component of integrated pest management programs for field-grown fruiting vegetables (29). Natural enemies provide an important yet often unnoticed service in agroecosystems by reducing pest populations. Further, effective biological control can increase action thresholds for insecticide applications to be used for management (113, 117).

Some of the significant challenges for greater reliance on biological control lie in understanding how environmental conditions affect predator-prey dynamics and overcoming the lag in establishment and increase of predator populations to suppress WFT populations effectively. The predatory mite, *Amblyseius swirskii*, is more effective in glasshouses than is *Neoseiulus cucumeris,* yet environmental conditions during the winter make releases of *N. cucumeris* more cost effective (45). In some cropping systems, reducing initial WFT populations with insecticides that are not disruptive to natural enemies allows augmentative biological control to succeed in a cost effective manner (98). Other tactics to increase predator populations before damaging WFT populations occur include inoculative releases of predators when WFT are low (e.g., 101), or providing alternative food sources for predators, in the form of non-pest prey, pollen, or other dietary supplements to sustain predators before prey are available (51). However, pollen significantly increases reproductive success of WFT (103). Consequently, food supplements targeting beneficial arthropods need to be applied cautiously so as not to increase pest populations (139).

Other natural enemies may offer longer-term suppression of WFT populations rather than immediate pest reductions. Entomophilic nematodes in the genus *Thripinema* (Tylenchida:

Allantonematidae) are obligate parasites that sterilize thrips (39). Parasitism by *Thripinema* reduces feeding and the ability to transmit tospoviruses, and suppression of field and greenhouse populations of WFT by these nematodes has been demonstrated (39).

Insecticides

Despite developments in these integrated management tactics, insecticides remain the cornerstone of many WFT management programs (40, 100). Such reliance on insecticides is unfortunate because WFT populations have a propensity for developing insecticide resistance, and invasive populations may be resistant to a range of insecticides upon their establishment in new regions (40). Intensive insecticide use can also foster the spread of WFT by giving it a competitive advantage over other thrips species in invaded areas (149). The use of broad-spectrum insecticides for WFT management has destabilized established IPM programs for other pests of many crops because of resistance, resurgence, and secondary pest outbreaks (29, 79).

Efforts to manage resistance through rotation among chemistries with different modes of action are hampered in systems where too few efficacious insecticide classes are available (40, 100). Resistance management is also confounded by the widespread use of insecticide mixtures, which accelerates evolution of resistance to multiple insecticide classes (21). The most effective strategy for resistance management is to only apply insecticides as needed within an overall integrated management program (40). Consequently, investment in IPM technologies for WFT should be enhanced because growers benefit from implementing IPM practices (84).

Future Challenges and Opportunities

WFT emerged as one of the first globally invasive polyphagous pests that resulted from international trade of agricultural products. Its spread has generated considerable research concerning its biology and behavior with the intent of developing new management approaches. Nevertheless, many growers remain focused on efforts to control WFT and the viruses it transmits intensive insecticide use. This control approach has destabilized established pest management programs creating unsustainable practices that have resulted in resistant WFT populations, resurgence and secondary pest outbreaks, and environmental degradation (79). This insecticide-reliant control approach has been widely adopted in recently invaded regions, leading to repetition of the problems encountered earlier by growers in other areas (145).

Further, anthropogenic environmental changes are expected to increase the prevalence and pest status of WFT. WFT populations flourish in ephemeral, disturbed habitats that often result from agricultural activities (38). Increased atmospheric CO_2 concentrations (44) and warming from global climate change (57) are likely to promote further spread of WFT, and increase its reproductive success and consequent pestiferousness.

Emerging technologies offer opportunities for improved management of WFT. Hyperspectral imaging coupled with machine learning-based assessments may allow rapid detection of either TSWV-infected or WFT-infested plants in a crop (116, 146). While these systems are currently at a "proof of concept" stage, they present possibilities for efficient detection of infestations, especially at low densities. Subsequent precision application of therapeutic management tactics, including insecticides, could be automated and coupled to monitoring systems to improve speed and efficiencies, making them practical for large-scale systems (146). Such precision management would reduce insecticide use and production costs. Additional benefits would accrue from less exposure of workers to pesticides, preservation of natural enemies, and increased sustainability of pest management programs.

The recent emergence of "-omics" (e.g., genomics, metabolomics, proteomics) tools may have potential for better understanding the biology and behavior of WFT. The results of molecular-level research may provide novel insights. Metabolomics research has identified relationships and interactions among different defensive compounds that may facilitate the selection for and development of cultivars with resistance to WFT (59, 60). Proteomic techniques have identified proteins that are either upregulated or downregulated in response to exposure of WFT larvae to TSWV (90). These have also identified complex mechanisms underlying resistance to the insecticide chlorpyrifos (147). These recent findings demonstrate the potential of "-omics" tools to fundamentally improve our understanding of WFT biology and dramatically advance our ability to manage this pest with environmentally-sound and sustainable methods.

Gene editing tools (e.g., CRISPR) may also have potential in the development of future WFT control programs. WFT is one of the first twenty-eight arthropod species selected for the "I5K Pilot Project," in which researchers are collaboratively sequencing the genome of each species (https://www.hgsc.bcm.edu/arthropods/i5k). This and other WFT genome projects are beginning to yield promising results. An initial interference RNA (RNAi)-based approach has been developed as a means to study WFT gene function and has allowed manipulation resulting in greater mortality rates and reduced fertility (5).

In an alternative approach, a natural bacterial endosymbiont of WFT, BFo2, has been employed to deliver RNAi (143). Because of the non-traumatic delivery, this method offers great potential to identify gene function and deliver RNAs that disrupt critical gene functions as a pest management tactic. Another system utilizes leaf discs for bioassays rather than whole transgenic plants to identify effector genes governing WFT reproductive performance (1). The ability to screen numerous genes under tightly controlled environmental conditions could greatly facilitate the identification of genes for resistance against WFT or tospovirus infection.

The promise of new control technologies as discussed above, may propel a fundamental shift of focus from killing WFT, to managing WFT populations and tolerating low density populations and an appropriate degree of injury. Such knowledge-based systems require long-term research and extension investments to familiarize growers with the benefits of emerging technologies (29). Appropriate funding for research and for training of public and private pest management specialists is necessary to develop and implement economically and ecologically sustainable management programs for WFT. These types of financial investments are going to be critical because of mounting concerns over food security, especially in developing nations, where the importance of WFT as a pest will continue to escalate (140). As greater agricultural production is required to meet the needs of a growing human population, it will be essential to adopt truly comprehensive IPM approaches.

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