

## Thrips: Pests of Concern to China and the United States

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### Abstract

Thrips are among the most important agricultural pests globally because of the damage inflicted by their oviposition, feeding, and ability to transmit plant viruses. Because of their invasiveness, a number of pest species are common to both China and the United States and present significant challenges to growers of a wide range of crops in both countries. Among the pest thrips common to both countries are four of the major global thrips pests, *Frankliniella occidentalis* (Pergande), *Scirtothrips dorsalis* Hood, *Thrips palmi* Karny, and *Thrips tabaci* Lindeman. This review addresses characteristics that enable thrips to be such damaging pests and how biological attributes of thrips create challenges for their management. Despite these challenges, a number of successful management tactics have been developed for various cropping systems. We discuss some of these tactics that have been developed, including the use of cultural controls, biological controls, and judicious use of insecticides that do not disrupt overall pest management programs. The exchange of this type of information will help to facilitate management of pest thrips, especially in regions where species have recently invaded. A prime example is *F. occidentalis*, the western flower thrips, which is native to the United States, but has recently invaded China. Therefore, management tactics developed in the United States can be adapted to China. Because further success in management of thrips requires a thorough understanding of thrips ecology, we discuss areas of future research and emphasize the importance of collaboration among different countries to enhance our overall understanding of the biology and ecology of thrips and to improve management programs for these widespread pests.

**Key words:** *Frankliniella*, *Scirtothrips*, *Thrips*, *Tospovirus*, behavioral ecology, pest status, integrated pest management

### OVERVIEW OF THRIPS AS PESTS

Thrips are minute insects (generally between 1 to 4 mm in length), but some species are among the most significant agricultural pests globally. This group includes many of the most important pests, and potential pests, affecting China and the United States (Table 1). However, it would be inaccurate to portray all members of the

order as pests, as fewer than 100 species are economically important pests (Mound 1997). A number of other thrips species are predatory, including ones that are beneficial as biological control agents of arthropod pests (Cox *et al.* 2006). Some phytophagous species are host specific and are proving valuable for biological control of invasive weeds (Simmonds 1933; Buckingham 1996; Mound *et al.* 2010). Far more species, though, are innocuous to humans, and therefore virtually nothing is known of their biology.

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Thrips comprise the order Thysanoptera, of which there are presently over 5 500 described species. The order is divided into two suborders, the Tubulifera and Terebrantia. Approximately 60% of the species are in the Tubulifera, which contains a single family, the Phlaeothripidae. There are eight recognized, extant families in the Terebrantia: Uzelothripidae, Merothripidae, Aeolothripidae, Adiheterothripidae, Melanthripidae, Fauriellidae, Heterothripidae, and Thripidae (Mound and Morris 2007). The order Thysanoptera is considered a monophyletic taxon, primarily based on the asymmetric mouthparts, where only the left mandible is fully developed and functional. The two suborders of Tubulifera and Terebrantia also are well-founded based on differences in ovipositor shape, wing structure, and the number of immature stages. Beyond that, the phylogeny of thrips is poorly understood and requires more study to establish a predictive classification of relationships within the order (Mound and Morris 2007).

Almost all species of pest thrips (>90%) are in the Terebrantian family Thripidae (Moritz *et al.* 2004b). Only a few species of Phlaeothripidae are considered to be pests. These include *Gynaikothrips ficorum* (Marchal) and *Gynaikothrips uzeli* (Zimmerman) as pests of *Ficus*, and *Haplothrips* spp., which include pests of grains in Europe and central Asia. Because the primary agricultural pests are species in the family Thripidae, this review will focus on the biology, ecology and management of those pest species. A number of pest species are common to both China and the United States. These include four of the major global thrips pests, *Frankliniella occidentalis* (Pergande), *Scirtothrips dorsalis* Hood, *Thrips palmi* Karny, and *Thrips tabaci* Lindeman.

These particular species have become global pests as they have been transported on agricultural produce. The onion thrips, *T. tabaci*, is possibly one of the earliest known examples of an invasive species, as it was spread on garlic and onions transported by Roman armies across the Roman Empire (Mound 2005). The western flower thrips *F. occidentalis*, which is native to western North America, received little attention as a pest until a pesticide resistant strain emerged from California greenhouses in the 1970's and subsequently spread rapidly around the world (Kirk and Terry 2003;

Reitz 2009). Since 1980, *F. occidentalis* has been the most intensively studied species of Thysanoptera, accounting for over one third of the publications on the order (Reitz 2009).

At present in the United States, *F. occidentalis* is distributed throughout the western United States (its native range), Hawaii and the southern and eastern United States. Its emergence in the eastern and southern United States coincided with its global range expansion (Kirk and Terry 2003). In China, *F. occidentalis* was first intercepted in quarantine in Kunming in 2000 (Jiang *et al.* 2001), and was then found to be established in pepper greenhouses in Beijing (Zhang *et al.* 2003; Lei *et al.* 2004; Ren *et al.* 2006). Subsequently, its known distribution in China has rapidly expanded. It has been reported in Lincang, Yunnan Province (Xu and Wei 2005), Qingdao, Shandong Province (Zheng *et al.* 2007), Hangzhou, Zhejiang Province (Wu *et al.* 2009), Nanjing, Jiangsu Province (Yan *et al.* 2010), Guiyang, Guizhou Province (Yu *et al.* 2009), and Yingchuan, Ningxia Province (Li *et al.* 2009).

In a similar situation, *T. palmi* was largely restricted to its native region of southern Asia before 1980, but since then it has spread throughout tropical and subtropical areas around the world, as well as temperate greenhouse production systems (Murai 2002; Cannon *et al.* 2007). It occurs in two of the United States, Hawaii and Florida (Johnson 1986; Tsai *et al.* 1995), and is present in at least 15 provinces in China, including Zhejiang, Hunan, Guangdong, Guangxi, Hainan, Sichuan, Yunnan, and Tibet (Han 1997). *Scirtothrips dorsalis* is another species that had limited distribution in its native range of southern Asia until recently (Vierbergen and Reynaud 2005). This thrips is a common pest thrips in southern China, in particular in Guangdong, Guangxi, Hunan, Jiangxi, Fujian, Anhui and Yunnan provinces (Han 1997). In the United States, *S. dorsalis* was first discovered in Hawaii in 1987; subsequently, it was found in Florida in 2005 and continues to spread through the southern United States (Ludwig 2009; Edwards *et al.* 2010). Although these four species are among the most widespread and important pest thrips, many other species are regionally important pests (Table 1). These other species share similar characteristics with the major global pests, and hence could yet become global pests as well.

**Table 1** Major thrips pests of significance to China and the United States<sup>1)</sup>

Species	Pest status		<i>Tospoviruses</i> vectored <sup>2)</sup>
	China	The United States	
<b>Family Phlaothripidae</b>			
<i>Gynaikothrips ficorum</i> (Marchal)	Ficus*	Ficus*	
<i>Gynaikothrips uzeli</i> Zimmerman	Ficus*	Ficus*	
<i>Haplothrips aculeatus</i> (F.)	Grains, rice*	Grains, rice*	
<i>Haplothrips tritici</i> Kurdjumov	Wheat*	-	
<i>Hoplothrips fungosus</i> Moulton	Mushroom*	-	
<i>Liothrips vaneeckei</i> Priesner	Xinjiang fritillary*	-	
<b>Family Thripidae</b>			
<i>Anaphothrips obscurus</i> (Muller)	Maize, grains*	Grains, grasses*	
<i>Anaphothrips sudanensis</i> Trybom	Cereals*		
<i>Aptinothrips stylifer</i> Trybom	Barley*		
<i>Caliothrips fasciatus</i> (Pergande)	-	Legumes, citrus*	
<i>Ceratothripoides claratris</i> (Shumsher)	-	-	CaCV
<i>Chirothrips manicatus</i> Haliday	-	Grasses*	
<i>Dendrothrips ornatus</i> (Jablonowski)	Lilac**		
<i>Dichromothrips corbetti</i> (Priesner)	Orchids***		
<i>Dichromothrips smithi</i> (Zimmerman)	Orchids***		
<i>Drepanothrips reuteri</i> Uzel	Grape*	Grape**	
<i>Echinothrips americanus</i> Morgan	-	Greenhouse and landscape ornamentals*	
<i>Frankliniella fusca</i> (Hinds)	-	cotton, groundnut, tobacco, tomato***	TSWV
<i>Frankliniella intonsa</i> (Trybom)	Ornamentals, rice***	forage legumes, ornamentals, vegetables*	INSV, GRSV, TCSV, TSWV
<i>Frankliniella occidentalis</i> (Pergande)	Tree fruits, small fruits, Ornamentals, vegetable***	Tree Fruits, small fruits, ornamentals, vegetable***	TSWV, INSV, ANSV
<i>Frankliniella schultzei</i> (Trybom)	-	Ornamentals, vegetables**	GRSV, TSWV
<i>Frankliniella tenuicornis</i> (Uzel)	Rice*	Yes	
<i>Fulmekiola serrata</i> (Kobus)	Sugarcane*	-	
<i>Heliothrips haemorrhoidalis</i> (Bouché)	-	Avocado, ornamentals*	
<i>Hercinothrips femoralis</i> (Reuter)	-	Banana, cotton, ornamentals, sugarcane, vegetables**	
<i>Lefroythrips lefroyi</i> (Bagnall)	Tea*	-	
<i>Limothrips cerealium</i> Haliday	-	Grains*	
<i>Megalurothrips distalis</i> (Karny)	Groundnut, legumes, ornamentals**	-	
<i>Megalurothrips usitatus</i> (Bagnall)	Legumes***	-	
<i>Microcephalothrips abdominalis</i> (Crawford)	Daisy*	Ornamentals*	TYRV
<i>Odontothrips</i> spp.	Alfalfa, clover**	-	
<i>Pseudodendrothrips mori</i> (Niwa)	Mulberry*	-	
<i>Psilothrips indicus</i> Bhatti	China wolfberry*	-	
<i>Rhipiphorothrips cruentatus</i> Hood	Grape, rose, wax apple***	-	
<i>Scirtothrips aurantii</i> Faure	-	-	
<i>Scirtothrips citri</i> (Moulton)	-	Citrus, small fruits**	
<i>Scirtothrips dorsalis</i> Hood	Citrus, cotton, melon, ornamentals, small fruits, tea, vegetables***	Citrus, cotton, melon, ornamentals, small fruits, tea, vegetables***	GBNV, GYSV, GCFSV
<i>Selenothrips rubrocinctus</i> (Giard)	Litchi, mango**	Avocado*	
<i>Sericothrips variabilis</i> Beach	-	Soybean*	
<i>Stenchaetothrips biformis</i> (Bagnall)	Rice, sugarcane, grains, Weeds, maize*	-	
<i>Taeniothrips inconsequens</i> (Uzel)	-	Sugar maple**	
<i>Thrips atratus</i> Haliday	Ornamentals*	Ornamentals*	
<i>Thrips flavidulus</i> (Bagnall)	Apple*	-	
<i>Thrips flavus</i> Schrank	Cotton*	-	
<i>Thrips hawaiiensis</i> (Morgan)	Banana, citrus, ornamentals, tea, tobacco***	Citrus, ornamentals*	
<i>Thrips palmi</i> Karny	Ornamentals, melons, vegetables***	Ornamentals, melons, vegetables***	CCSV, CACV, MYSV, GBNV, WBNV, WSMoV
<i>Thrips simplex</i> (Morison)	Oil tung, gladiolus***	Gladiolus*	
<i>Thrips tabaci</i> Lindeman	Onion, cotton, tobacco, Ornamentals, vegetables***	Onion, cotton, tobacco, Ornamentals, vegetables***	IYSV, TSWV
<i>Thrips vulgatissimus</i> Haliday	Barley, wheat, buckwheat*	Wheat*	

<sup>1)</sup> This list includes species that are established in either country are included as are known invasive species that are likely to become established. Relative importance as a pest: \*, minor pest; \*\*, moderate pest; \*\*\*, major pest of concern.

<sup>2)</sup> See Table 2 for explanations of virus acronyms.

## LIFE CYCLE OF PEST THRIPS

The general life cycles of Terebrantian thrips are similar to one another. The life stages consist of the egg, two active feeding larval instars, two quiescent, non-feeding instars, the propupa and pupa, and the adult. In addition to these stages, Tubuliferan thrips have a second pupal stage. Thripidae females use their saw-like ovipositor to make an incision into plant tissue and then the egg is embedded into the incision (Lewis 1973). Thripidae females may lay eggs in any non-woody aboveground plant tissue, including stems, foliage, flowers, and fruits. Adults and larvae tend to occupy similar ecological niches and feed on similar host resources (Kirk 1997). The spatial distribution of adults and larvae within plants may differ (Reitz 2002; Mo *et al.* 2008), but adults and larvae tend to prefer concealed, protected habitats on plants, such as flowers, buds, or where leaves are appressed to one another (Lewis 1973). This highly thigmotactic behavior can make it difficult to detect infestations on plants and to successfully treat infestations with contact insecticides. Likewise because eggs of Terebrantian thrips are embedded in plant tissues, they are difficult to detect and are not very susceptible to fumigation (MacDonald 1993; Janmaat *et al.* 2002; Simpson *et al.* 2007). The non-feeding pupal stages are generally found off plants in leaf litter or the top layer of soil, but pupae may also remain on plants, especially those with complex floral architecture (Buitenhuis and Shipp 2008).

Most pest species are highly polyphagous, in terms of the number of plants that adults of a particular species are known to feed. These polyphagous species have been portrayed as phytophagous opportunists that exploit ephemerally available hosts, both temporally and spatially (Mound and Teulon 1995). Therefore, one of the most important aspects to understanding thrips biology and ecology is proper characterization of the reproductive hosts of a species. From an ecological perspective, reproductive hosts are those that support significant larval development so that population growth rates would be positive. However, most host associations are based on recordings of adults on particular plants (Mound 2005). These data are important in pest management terms for understanding which crops may be susceptible to damage, but they are of limited use in

understanding sources of thrips populations. Some field studies have examined the association of larvae and adults with plants (Yudin *et al.* 1986; Milne and Walter 1998; Groves *et al.* 2002; Painsi *et al.* 2007; Northfield *et al.* 2008; Wu *et al.* 2009; Zhi *et al.* 2010). These studies clearly indicate that adults can occur in large numbers on plants where reproduction is minimal, and that certain plants are more suitable reproductive hosts than others. A number of laboratory assays have confirmed that reproductive success varies widely across hosts (Tsai *et al.* 1995; de Kogel *et al.* 1997; Zhi *et al.* 2010). However, no selective study can completely characterize the breeding range of any particular species. A great challenge in characterizing the reproductive biology and host plant relationships of thrips has been a lack of robust taxonomic keys for the immature stages of thrips. Results of field studies often include data on separate species for adults, but pooled larval data. Studies in which field collected larvae have been reared to adulthood for identification are subject to biases from differential mortality under laboratory rearing conditions. One approach that is being developed to circumvent the need for morphological keys is the use of molecular genetic identification methods (Moritz *et al.* 2004b; You *et al.* 2007). These methods have the advantages of being able to be used for the identification of all ontogenetic stages and requiring the use of standard molecular analysis techniques rather than specialized taxonomic expertise. These molecular analyses will be employed more widely as their costs continue to decline.

A further complication in the understanding of species host ranges lies in their intraspecific variation, including populations with differing host affinities. While this variation is not unexpected among such cosmopolitan pests, biologically distinct populations of the same species may exist within the same geographic area. Within *T. tabaci*, rearing experiments have demonstrated that populations can be better adapted to certain plants than others, leading to host associated genetic differentiation (Chatzivassiliou *et al.* 2002, Brunner *et al.* 2004). Host associated populations have also been reported for *F. occidentalis* (de Kogel *et al.* 1997), with some populations outperforming others on certain hosts. These results underscore the importance of evaluating thrips responses under varying local conditions.

Not only is there evidence of polymorphisms within

species, but several authors have posited that some widespread species of pest thrips are actually cryptic species complexes. Most notably, recent evidence indicates that *F. occidentalis* is a complex of two cryptic species (Rugman-Jones *et al.* 2010). The “*Lupinus*” strain of *F. occidentalis* was originally reported in New Zealand as occurring on *Lupinus arboreus* imported from California, but it has not been found on other crops and has not been considered a pest. In contrast, the global “glasshouse” (=greenhouse) pest strain (Immaraju *et al.* 1992) was introduced to New Zealand in 1992 and rapidly became a pest on numerous crops, as has occurred elsewhere in the world (Martin and Workman 1994; Teulon and Nielsen 2005). The glasshouse (=greenhouse) strain has much higher reproductive rates than the “*Lupinus*” strain (Nielsen *et al.* 2010) and is more resistant to insecticides (Martin and Workman 1994). These differences suggested the two were different types, and this has been confirmed by recent molecular data, which show these are two distinct species that have sympatric origins in the western United States and have different host ranges (see below, Rugman-Jones *et al.* 2010). The two species overlap in their color polymorphisms and are sympatric in California. Although both species appear to have invaded China, the so-called glasshouse species appears to be the most widely distributed and to account for most pest damage attributed to “western flower thrips” around the world. There is evidence that *S. dorsalis* is also a cryptic species complex (Rugman-Jones *et al.* 2006), and the same may be true of *T. tabaci* (Brunner *et al.* 2004). The findings that these global pest species are likely species complexes highlight the importance of preserving voucher specimens for future morphological and genetic study. It further indicates that there may often be a need to replicate key biological studies in space and time rather than assuming that biological traits observed for one population are uniform for a particular species.

The polyphagous nature of pest thrips species has important implications for their management, especially for the use of insecticides for their management. Broad-scale insecticide resistance has been well documented in *F. occidentalis* (Jensen 2000; Bielza 2008) and in *T. tabaci* (Shelton *et al.* 2006). Because they are polyphagous, pest thrips species generally have an array of metabolic pathways to detoxify plant secondary

compounds, which can serve as preadaptations to detoxify insecticides (Rosenheim *et al.* 1996). Certain enzyme systems are sufficiently generalized to confer cross-resistance to multiple classes of insecticides (Espinosa *et al.* 2005). The haplo-diploid mode of reproduction contributes to the rapid development of resistance in populations because the alleles of the hemizygous males are exposed directly to selection (Denholm *et al.* 1998). It is possible that resistance could develop rapidly in thelytokous populations of *T. tabaci* because of limited genetic variation in such populations. Nault *et al.* (2006) observed that there was no difference in susceptibility of arrhenotokous and thelytokous *T. tabaci* populations to two insecticides. Because of rapid development rates and the threat of insecticide resistance development, most current insecticide resistance management programs for thrips recommend that growers avoid making successive applications of materials with the same mode of action or potential resistance mechanism (Bielza 2008; Funderburk 2009).

## DIET AND FEEDING BEHAVIOR

Obviously, observable damage to plants in the form of feeding scars on petals, leaves or fruit gives an indication of the diet of thrips. However, thrips species may have broader and more mixed diets than that suggested by observable damage. A number of species are known to feed on pollen (Kirk 1984), and some species considered to be phytophagous are facultatively predaceous (Kirk 1997). The inclusion of pollen in the diet can stimulate oviposition, reduce larval development time, and increase female fecundity (Trichilo and Leigh 1988; Kirk 1997; Hulshof and Vanninen 2002; Hulshof *et al.* 2003; Zhi *et al.* 2005; Riley *et al.* 2007). Although primarily phytophagous, adults and larvae of several pest species, including *F. occidentalis*, *Frankliniella schultzei* (Trybom), *Thrips imaginis* Bagnall, and *T. tabaci*, will prey on eggs of spider mites, *Tetranychus urticae* Koch (Trichilo and Leigh 1986; Wilson *et al.* 1996). This characteristic makes thrips potentially valuable as biological control agents in crops such as cotton (*Gossypium hirsutum* L.) where spider mites may be a more serious pest than thrips (Wilson *et al.* 1991).

Pollen and arthropod prey are thought to provide additional nitrogen in the diet of thrips, and Kirk (1997) has suggested that the quest for adequate nitrogen may explain why so many thrips breed in leaf buds rather than on mature leaves, which typically have lower nitrogen content than emergent foliage (Mattson 1980; Kursar and Coley 1991). A notable exception to this pattern is *Heliothrips haemorrhoidalis* Bouché. It favors mature foliage over young foliage, yet its feeding and oviposition within those sites are positively related to nitrogen content (Scott Brown *et al.* 2002).

## IMPLICATIONS OF NITROGEN TO THRIPS POPULATIONS AND PLANT DAMAGE

Because nitrogen is a key nutritional component in thrips diets and agricultural crops tend to be highly fertilized, there has been considerable interest in the relationship between plant nitrogen content and thrips populations. Because oviposition rates and fecundity increase with host nitrogen content, thrips populations can flourish on highly fertilized crops that are reproductive hosts (Schuch *et al.* 1998; Davies *et al.* 2005). *Frankliniella occidentalis* larvae feed more intensively on plant tissue with higher concentrations of aromatic amino acids, soluble carbohydrates and protein (Mollema and Cole 1996; Wu *et al.* 2007). In addition, increased nitrogen content of plants can further enhance pest damage to non-reproductive hosts. For example, tomato, *Solanum lycopersicum* (Mill.), is a poor reproductive host for *F. occidentalis*, yet adult populations increase on it as nitrogen fertilization of the crop increases (Brodbeck *et al.* 2001; Baez *et al.* 2011). These results indicate that thrips are capable of exerting a degree of active host plant selection and are not solely passive dispersers.

As alluded to above, only the left mandible in thrips is developed and functional. When feeding on plant tissue, individuals puncture individual cells with the mandible and then use the maxillary stylets to extract the fluid from those cells (Chisholm and Lewis 1984; Hunter and Ullman 1989; Kindt *et al.* 2003). The same process is repeated when feeding on foliage, floral tissue, fruits, or pollen grains (Kirk 1984). Adults and larvae feed in a similar manner, so both stages contribute to plant damage. Individuals tend to feed in local-

ized areas, which results in silvered or necrotic patches on foliage, flowers and fruit. Feeding within developing buds leads to deformation of leaves or flowers (Childers 1997).

## MODES OF REPRODUCTION

Most Thysanoptera are arrhenotokous, with females developing from fertilized eggs and males developing from unfertilized eggs (Moritz 1997). There is little information on primary sex ratios (i.e., sex ratio of eggs) for most species, but it is approximately 1:1 for *F. occidentalis* (Terry and Kelly 1993). Despite even primary sex ratios, sexually reproducing species often show biased sex ratios of adults in field collections. These biases are not thought to result from females actively controlling the sex of their progeny (Terry and Kelly 1993). It is more likely that biased adult sex ratios are a function of differences between the sexes in their dispersal, distribution in response to host quality and longevity, with females being longer lived than males (Higgins and Myer 1992; Sims *et al.* 2009). Higgins and Myer (1992) proposed that populations of *F. occidentalis* early in the season in greenhouses would be male biased because the founder females may be virgins and thus produce only sons initially. As populations expand and female mate and produce daughters, sex ratios would become more female biased. Consequently, they propose that adult sex ratios could be used to predict future population trends and time management tactics. Recently, it has been shown that the proportion of adult females in cohorts of *F. occidentalis* increases with temperature (Kumm and Moritz 2010), but in contrast, temperature does not seem to influence adult sex ratios in *T. tabaci* (Nault *et al.* 2006). Other biotic factors can also alter sex ratios. Differential susceptibility of males to predation may increase the female bias in sex ratios of *F. fusca* (Data not shown). Likewise, parasitism by the entomogenous nematode *Thripinema fuscum* Tipping & Nguyen reduces longevity of male *F. fusca* but not of females (Sims *et al.* 2009) and thus produce female biased sex ratios.

One notable exception to the general pattern of arrhenotokous sexual reproduction is *T. tabaci*. Individuals of this cosmopolitan species may reproduce ei-

ther sexually or asexually. Many populations are thelytokous, in which males do not occur and females are produced from unfertilized eggs. However, certain populations of *T. tabaci* may consist of arrhenotokous, thelytokous, and deuterotokous individuals, in which both males and females are produced from unfertilized eggs (Nault *et al.* 2006). It is uncertain what controls parthenogenesis in *T. tabaci*, but in other species, thelytoky is triggered by the endosymbiotic bacteria *Wolbachia* (Kumm and Moritz 2008).

## FECUNDITY AND IMMATURE DEVELOPMENT

As with other arthropods, temperature has a great effect on development rate of thrips. Minimum developmental thresholds have been determined for many pest species, allowing for temperature-driven developmental models to be constructed (Lu and Lee 1987; Rhodes *et al.* 1989; Tataru 1994; van Rijn *et al.* 1995; Jarosik *et al.* 1997; Katayama 1997; Ekesi *et al.* 1999; Stacey and Fellowes 2002; Chhagan and Stevens 2007; Liu *et al.* 2008; Park *et al.* 2010). At favorable temperatures of 25–30°C, egg to adult development time can be as brief as 9–13 d (Lublinkhof and Foster 1977; Robb 1989; Gaum *et al.* 1994; Katayama 1997; Reitz 2008). Female thrips continue to lay eggs throughout adulthood, and under laboratory conditions, can be long-lived (Trichilo and Leigh 1988; Tataru 1994; Murai 2001; Hulshof and Vanninen 2002; Zhi *et al.* 2005; Reitz 2008). These characteristics allow for multiple, overlapping generations of these opportunistic species to develop on available host resources. *F. occidentalis* does not have an obligatory developmental or reproductive diapause (Ishida *et al.* 2003). Therefore, development and oviposition occur whenever temperatures exceed a minimum threshold, which is in the range of 8–11°C for most pest species (Katayama 1997; McDonald *et al.* 1998). Some species undergo reproductive diapauses that are regulated by critical photoperiods (Kamm 1972; Ekesi *et al.* 1999; Nakao 1999). Still, further research is needed on geographic differences within species on their climatic tolerances and the effects of temperature, photoperiod on reproduction (Stacey and Fellowes 2002).

## POPULATION BIOLOGY

Pest thrips fit the classic definition of *r*-strategists, as they tend to exploit ephemeral, unpredictable resources, have high reproductive rates, short generation times, and are highly vagile (Pianka 1970). High levels of female fecundity lead to high intrinsic rates of population increase, so that populations can increase rapidly (Gaum *et al.* 1994; Gerin *et al.* 1994; Hulshof *et al.* 2003). This capacity for increase becomes apparent in the absence of natural enemies, as when insecticides, which pest thrips may be resistant to, are applied to crops intensively. Thus, in many circumstances, thrips can be regarded as secondary pests that become problematic when populations are released from natural controls.

For many years it has been argued that natural enemies have little ability to regulate thrips populations (Davidson and Andrewartha 1948; Parrella and Lewis 1997), especially in cropping systems because of the high reproductive rate of thrips and the inability of natural enemies to compensate for this intrinsic population growth in a timely manner. However, recent evidence points to the importance of population regulation by natural enemies and the possibility that pest problems often emerge when thrips are released from regulation by their natural enemies. Most of the research on interactions between thrips and natural enemies has focused on predatory insects and mites. Funderburk *et al.* (2000) were the first to show the important regulatory effects of the predator *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) on *Frankliniella* spp. under field conditions. Two factors make this predator an effective biological control agent. It has a high predation rate and it rapidly tracks thrips populations as thrips colonize newly available host resources (Ramachandran *et al.* 2001). *Orius insidiosus* is such an important naturally occurring predator, that management plans for vegetables like pepper and eggplant are centered on the conservation of *O. insidiosus* (Reitz *et al.* 2003; Funderburk 2009). Other studies have shown the importance of *O. insidiosus* and other related species as biological control agents of thrips in greenhouse crops (van den Meiracker and Ramakers 1992; Kawai 1995; Jacobson 1997; Bosco *et al.* 2008). In China, nymphs

and adults of *Orius sauteri* (Poppius) are important predators of *F. occidentalis*. Laboratory experiments have demonstrated that *O. sauteri* prey on *F. occidentalis* larvae and adults, indicating that *O. sauteri* might act as a key predator of *F. occidentalis* under field conditions (Zheng *et al.* 2007; Sun *et al.* 2009; Xu and Enkegaard 2009). Sabelis and van Rijn (1997) presented a model of predator-prey dynamics between *O. insidiosus* and *F. occidentalis*. Their model showed the conditions and predator-prey ratios necessary for *O. insidiosus* to drive a population of *F. occidentalis* to local extinction. Although theoretical, the model estimates are similar to levels seen experimentally. Therefore, these models may be useful in guiding integrated pest management (IPM) programs focused on the reliance on *Orius* spp., and a number of *Orius* spp. are commercially available for release in greenhouses around the world.

Another group of natural enemies that can have significant impacts on thrips population dynamics are predatory mites in the families Phytoseiidae and Laelapidae. Little is known of their interactions with thrips in natural environments, but there has been considerable interest in their application as biological control agents, especially in protected (glasshouse/greenhouse) environments. Most phytoseiid mites are plant dwelling generalist predators so that they can survive on alternative prey (or pollen) when thrips populations are low. Because of their small size, these mites typically prey on young thrips larvae (Sabelis and van Rijn 1997). Mites in the family Laelapidae, especially *Hypoaspis miles* (Berlese) dwell in the soil and so prey on thrips pupae (Berndt *et al.* 2004). These soil dwelling species can complement control from plant dwelling predators to enhance suppression of pest thrips populations. At present, several species of phytoseiid and laelapid mites are commercially produced for release in cropping systems. The selection of phytoseiid agents for release depends on the host plant because plant resources, such as pollen, affect predator success (Messelink *et al.* 2006). One benefit from using predatory mites is that their polyphagous nature may enable them to contribute to management of multiple pests, not just thrips (Gillespie and Quiring 1992; Calvo *et al.* 2010).

A number of parasitoids that parasitize various thrips

species have been discovered and there has been interest in their potential as classical biological control agents for invasive thrips (Loomans *et al.* 1997). All known parasitoids are either parasitoids of eggs or larvae in the hymenopteran superfamily Chalcidoidea. Despite field surveys showing high levels of parasitism (Hirose *et al.* 1993), parasitoids have not been found to be very effective in controlling thrips populations (Loomans *et al.* 1997). Although there has been some impact from the release of *Thripobius semiluteus* Boucek as a classical biological control agent against *Heliothrips haemorrhoidalis* in avocados (*Persea americana*) in California, it has not provided sufficient control (McMurtry *et al.* 1991). The lack of effective biological control by parasitoids may be a result of the small size of parasitoids, which limits their dispersal ability and their high susceptibility to insecticides (Hirose *et al.* 1993). In an extensive qualitative survey for parasitoids of *F. occidentalis* in Europe and its native range in North America, Loomans (2006) found the predominant species to be *Ceraninus menes* (Walker) (Hymenoptera: Eulophidae). However, this parasitoid was typically recovered in uncultivated habitats and not within agricultural fields.

Until recently, there has been little information on fungal pathogens of thrips. Although natural epizootics have rarely been detected, a number of different fungi have been isolated from thrips (Butt and Brownbridge 1997). These findings have made fungal pathogens another promising group of biological control agents as alternatives to harmful synthetic pesticides for thrips management, and several strains of entomopathogenic fungi have been developed worldwide for the control of many agricultural pests, including some for various species of thrips. *Beauveria bassiana* (Balsamo) Vuillemin has been considered one of the most effective entomopathogenic fungi against thrips (Brownbridge 1995). Several isolates of *B. bassiana* from China have been found to be highly virulent against *F. occidentalis* and are being developed as biological control agents (Zhang *et al.* 2009). However, the success of fungal entomopathogens as biological control agents depends not only on their efficacy against pests, but also on low virulence against non-target arthropods. Because *B. bassiana* has a broad host range, there are concerns that it could affect beneficial insects, such as



natural enemies of insect pests. Consequently, guidelines for the registration of biopesticides require laboratory testing for their infectivity to non-target organisms. Our recent research indicates that several isolates, which are being considered for commercial use to control thrips in China, do not negatively affect the development and survival of *O. sauteri* and would be compatible with this biological control agent (data not shown). Likewise, Jacobson *et al.* (2001) demonstrated that another strain of *B. bassiana* is compatible with the use of the predatory mite *Neoseiulus* (= *Amblyseius*) *cucumeris* (Oudemans) in greenhouse systems.

Recent research has addressed the importance of interspecific competition in thrips population dynamics. Field observations suggest that the presence of competing species limits abundance of *F. occidentalis* (Paini *et al.* 2007; Northfield *et al.* 2008; Funderburk 2009) and laboratory experiments show that larvae of the non-pest species *Frankliniella tritici* (Fitch) outcompete *F. occidentalis* (Paini *et al.* 2008). Therefore, conserving populations of non-pest thrips may mitigate the threat posed by significant pests, such as *F. occidentalis* (Funderburk 2009).

## VECTOR-VIRUS RELATIONSHIPS

The greatest threat of pest thrips is posed by the ability of some species to transmit plant viruses in the genus *Tospovirus* (Bunyaviridae). The type species, *Tomato spotted wilt virus* (TSWV), was first characterized by Samuel *et al.* (1930) and until the 1990s the genus was considered monotypic. Over the past 20 years, there has been a rapid increase in the number of recognized *Tospovirus* species and thrips vectors, including a better appreciation of their host plant range, vector affinities, and geographic distribution (Table 2). At present, eight species of *Tospovirus* are recognized by the ICTV ([www.ictvonline.org](http://www.ictvonline.org)), but over 20 species of *Tospovirus* have been described (Pappu *et al.* 2009). Of the described species, at least 15 species are present in southern Asia, which increases the risk of new species occurring in China. At present, 5 *Tospoviruses* are known to occur in China: TSWV, *Impatiens necrotic spot virus* (INSV), *Tomato zonate spot virus* (TZSV), *Capsicum chlorosis virus* (CaCV), and *Groundnut/Pea-nut yellowspot virus* (GYSV), with an additional three

occurring on the island of Taiwan (Su *et al.* 1987; Chen *et al.* 2003; Chen *et al.* 2007; Ding *et al.* 2007; Dong *et al.* 2008; Zhang *et al.* 2010). Four *Tospoviruses* are present in the United States: TSWV, INSV, *Iris yellow spot virus* (IYSV), and *Groundnut ringspot virus* (GRSV) (Pappu *et al.* 2009; Webster *et al.* 2010). Along with the expanding diversity of viruses, there is an expanding diversity of at least 12 species of thrips that are recognized as vectors of the various *Tospoviruses*.

Vector species have a complex relationship with these viruses. For an individual to successfully transmit a *Tospovirus*, it must acquire the virus as a larva, primarily as a first instar (Tsuda *et al.* 1996, van de Wetering *et al.* 1996). However, because larvae do not readily move from plant to plant, transmission is largely restricted to the adult stage. Because transmission can occur in as little as 5 min of feeding (Wijkamp *et al.* 1996), disease spread cannot be controlled by insecticides alone.

Because most *Tospoviruses* have only recently been recognized and described, little is known of their specific biology, host plant relationships and vectors. *Tomato spotted wilt virus* has one of the broadest host ranges of any plant pathogen, with over 1 000 species of plants in 84 families susceptible to it (Parrella *et al.* 2003). As evidence accumulates, it appears that other *Tospoviruses* will have large and diverse host ranges. For example, it was originally thought that IYSV was restricted to plants in the family Liliaceae, but it has been identified infecting over 50 species distributed across at least 12 families (Gent *et al.* 2006, [www.alliumnet.com](http://www.alliumnet.com)). Not all known hosts for these viruses support reproduction of vectors. Yet given the broad and diverse host ranges, it is likely that viruliferous adults arise from many different sources. A “relative inoculum potential index” has been developed by researchers in North Carolina to characterize plants as TSWV sources based on the degree of vector reproduction and likelihood of virus infection (Groves *et al.* 2002). This information is a critical step in understanding the epidemiology of thrips-transmitted viruses. Still needed is an understanding of the actual contribution of different source plants, which may contain different viral strains, to disease progress in different crops (Ullman *et al.* 2002). There is little information on how the transmissibility of different virus strains is affected by source and recipient plants. Behavioral responses of thrips to particular plants may also affect disease spread.

**Table 2** Tospoviruses, including those reported in China and the United States, and their known vectors<sup>1)</sup>

Virus <sup>2)</sup>	Occurrence in China and the United States	Known vectors (worldwide) <sup>3)</sup>
Alstroemeria necrotic streak virus (ANSV) (Hassani-Mehraban <i>et al.</i> 2010)		<i>Frankliniella occidentalis</i>
Calla lily chlorotic spot virus (CCSV)	Taiwan	<i>Thrips palmi</i>
Capsicum chlorosis virus (CaCV) CaCV-CP (Chen <i>et al.</i> 2007)	China	<i>Ceratothripoides claratris</i> , <i>T. palmi</i>
Chrysanthemum stem necrosis virus (CSNV) <i>Groundnut (Peanut) bud necrosis virus</i> (GBNV/PBNV) <i>Groundnut (Peanut) yellow spot virus</i> (GYSV/PYSV)	- China China	<i>Frankliniella occidentalis</i> , <i>F. schultzei</i> , <i>F. gemina</i> <i>F. schultzei</i> , <i>Scirtothrips dorsalis</i> , <i>T. palmi</i> <i>S. dorsalis</i>
<i>Groundnut ringspot virus</i> (GRSV) <i>Impatiens necrotic spot virus</i> (INSV)	United States (Webster <i>et al.</i> 2010) the China, United States	<i>F. intonsa</i> , <i>F. occidentalis</i> , <i>F. schultzei</i> <i>F. intonsa</i> , <i>F. occidentalis</i> , <i>F. schultzei</i>
<i>Iris yellow spot virus</i> (IYSV)	the United States	<i>T. tabaci</i>
Melon severe mosaic virus (MeSMV)	-	Unknown
Melon yellow spot virus (MYSV)	Taiwan	<i>T. palmi</i>
Peanut chlorotic fan-spot virus (PCFV)	Taiwan	<i>S. dorsalis</i>
Physalis silver mottle virus (PSMV)	-	Unknown
Polygonum ringspot virus (PoRSV)	-	<i>Dictyothrips betea</i> (Ciuffo <i>et al.</i> 2010)
<i>Tomato chlorotic spot virus</i> (TCSV)	-	<i>F. occidentalis</i> , <i>F. schultzei</i> , <i>F. intonsa</i>
<i>Tomato spotted wilt virus</i> (TSWV)	China, the United States	<i>F. bispinosa</i> , <i>F. cephalica</i> , <i>F. fusca</i> , <i>F. occidentalis</i> , <i>F. schultzei</i> , <i>Thrips setosus</i> , <i>T. tabaci</i>
Tomato zonate spot virus (TZSV)	China	Unknown
Tomato yellow ring virus (TYRV) (Ghotbi <i>et al.</i> 2005, Hassani-Mehraban <i>et al.</i> 2007)	-	<i>Microcephalothrips abdominalis</i> , <i>T. tabaci</i>
Watermelon bud necrosis virus (WBNV)	-	<i>T. palmi</i>
Watermelon silver mottle virus (WSMoV)	Taiwan	<i>T. palmi</i>
<i>Zucchini lethal chlorosis virus</i> (ZLCV)	-	<i>F. zucchini</i>

<sup>1)</sup> Updated from Pappu *et al.* (2009) and ICTV (<http://www.ictvdb.org/Ictv/index.htm>). Viruses listed as occurring in Taiwan are not known to occur in P.R.China.

<sup>2)</sup> Italicized names are recognized *Tospovirus* species. Other names that are not italicized are tentative species.

<sup>3)</sup> Vector species in bold are those associated with *Tospovirus* transmission in China, the United States, or both countries.

Disease incidence may increase in less preferred hosts compared with preferred host plants because non-preference may lead to increased interplant movement (Rhainds and Shipp 2003; Reitz 2005).

In addition to the emergence of newly recognized vector species, there is a growing awareness of intraspecific variation in vector competence. As discussed above, three different reproductive modes exist in *T. tabaci* (Nault *et al.* 2006), which has a bearing on vector competence (Chatzivassiliou *et al.* 2002). Individuals from arrhenotokous populations are able to transmit TSWV, but individuals from thelytokous populations are unable to transmit TSWV. Transmission efficiency of arrhenotokous populations is further mediated by their host plant origin. Populations derived from tobacco have significantly higher transmission efficiencies than those derived from leek. *Frankliniella schultzei* exists in two distinct color morphs. The dark morph is a competent vector of five different *Tospoviruses*, but the light morph is not a competent virus vector (Sakimura 1969; Whitfield *et al.* 2005). *Thrips palmi* populations in Asia are competent vectors of six known *Tospoviruses* (Pappu *et al.* 2009), but

populations in the United States of Florida and Hawaii do not transmit *Tospoviruses*. This could be a result of a competent vector species not being introduced with its viruses, or that populations of *T. palmi* in the United States are derived from genetically distinct lineages that are not able to vector *Tospoviruses* (Brunner *et al.* 2004; Morse and Hoddle 2006). Included in this scenario is that these cosmopolitan pest species are composed of cryptic species that vary in their vector competence.

The best control strategy, ideally, for insect-vectorated viruses is host plant resistance, and a broad array of research programs has addressed traditional plant breeding and transgenic approaches to resistance. There have been successes in the development of resistant crops, but there are important constraints in the development and use of resistant crops. For most crops, there are limited sources of naturally-occurring resistance. In the case of tomato, all commercially resistant lines are based on the *SW-5* gene. Unfortunately, this single dominant gene resistance (Boiteux and de Avila 1994) has not proved to be durable, with resistance breaking strains of the virus appearing in different geographic regions (Cho *et al.* 1995; Latham and Jones 1998; Aramburu

and Marti 2003). The same situation has occurred with pepper where a single gene (*TSW*) has been used to confer resistance. The failure of these lines to provide durable resistance has been attributed to the high genetic diversity of virus populations within any given geographic area and that these are very plastic RNA viruses (Best 1968; Mandal *et al.* 2006). Mandal *et al.* (2006) found that putatively resistant lines of groundnut, pepper, tobacco and tomato responded differently when challenged with two different isolates of TSWV, with responses on a continuum from susceptibility to maintaining resistance. Maris *et al.* (2003) have shown that pepper cultivars that are resistant to *F. occidentalis* can reduce secondary spread of TSWV because the vector is unable to successfully reproduce within the crop. While this strategy may be of use in greenhouse systems, it would not likely control primary spread, which is the predominant means of spread in open field crops (Puche *et al.* 1995). In onion, there is variation in susceptibility to IYSV, but to date no truly resistant lines have been identified (Diaz-Montano *et al.* 2010). In groundnut, several commercial varieties are less susceptible to TSWV than other varieties, and hence are widely planted in the southern United States. However, these “resistant” lines can show disease incidence in excess of 20% (Branch *et al.* 2003). Although this level of disease appears severe, it is much less than the >80% incidence that can occur in susceptible lines.

When confronted with a strong selective pressure from resistant plants, viral genetic diversity can lead to rapid selection for resistance breaking strains. Further complicating the development of resistant crops is the interspecific diversity of viruses and vectors in *Tospovirus* pathosystems. The *Tsw* gene in pepper appears to confer resistance only against certain isolates of TSWV, but not against GRSV and TCSV, two *Tospoviruses* that are closely related to TSWV (Boiteux and de Avila 1994). A novel approach to host plant resistance has been to combine natural plant resistance and transgenic resistance in a single plant line. Gubba *et al.* (2002) integrated *SW-5* resistance with transgenic nucleocapsid gene resistance in tomato. While promising, this approach provided resistance to some, but not all, strains of TSWV, GRSV, and TCSV used in the test challenges. These results suggest that host plant resistance is an extremely difficult management strategy to

implement and maintain. This will be especially true in regions that have a high diversity of *Tospoviruses*, such as Southeast Asia and elsewhere as *Tospoviruses* continue to spread around the world (Hanssen *et al.* 2010).

The issues involved in the use of host plant resistance simply highlight the need for integrated programs for management of thrips and for thrips-vectoring viruses in agroecosystems. Historically, there has been an intense reliance on insecticides for control of thrips in agricultural crops. There has also been a pervasive history of insecticide failures against thrips over the past 50 yr (Race 1961; Jensen 2000). Because no “thrips-specific” insecticides have been developed, most products for use against thrips have been formulated to combat other pests; hence they may not necessarily have high efficacy against thrips. Moreover because products may be used against multiple pests, treatments not targeting thrips can contribute to the development of resistance in thrips. The thigmotactic nature of most pest thrips further diminishes the efficacy of contact insecticides because of the inability to get adequate exposure. Further, there is evidence that certain insecticides can stimulate reproduction of the citrus thrips *Scirtothrips citri* Moulton (Morse and Zareh 1991). There is mounting evidence of such hormologotic effects being induced by synthetic pyrethroids in *F. occidentalis* (Frantz and Mellinger 2009; Funderburk 2009). Despite these problems, insecticides will continue to play an important role in thrips management. It is not a question of whether insecticides will be used; it is a question of using them judiciously as a component of an overall management program (Bielza 2008; Funderburk 2009). The following are examples of management programs that have been developed for different thrips in different agroecosystems.

## THRIPS MANAGEMENT IN FRUIT TREES

Feeding and oviposition by different thrips species can cause substantial damage in tree fruit crops. In western North America, *F. occidentalis* is the most damaging thrips species in apple, where the most significant damage is from females that disperse into orchards at key times during the bloom stage and oviposit (Terry 1991). Oviposition elicits a physiological wound response creating spots on developing fruit, which con-

tinue to expand as the fruit matures (Childs 1927). This aesthetic damage can reduce the marketability of the fruit. In other regions, direct feeding damage by species such as *Thrips imaginis* and *Taeniothrips inconsequens* (Uzel) has been reported to cause flower loss or unsuccessful pollination in apple (Childers 1997). Management of weeds to keep them from flowering and serving as sources of thrips within orchards may provide some cultural control of *F. occidentalis* populations (Cossentine *et al.* 1999), but this tactic appears limited given the scale of immigration that can occur from outside orchards (Pearsall and Myers 2001; Cockfield and Beers 2008). Because of the brief, but critical time that the crop is at risk, there is still a major reliance on insecticides to reduce thrips damage. However insecticides should be applied judiciously, with applications restricted to the petal fall stage to avoid interference with pollinators and to provide better control of thrips when the crop is at its most vulnerable stage (Degrandi-Hoffman *et al.* 1988; Cockfield *et al.* 2007). Feeding damage, primarily by larvae, is more significant on stone fruits than on apple. Pearsall (2000) determined that the critical time for larval feeding damage in nectarines in western North America is at petal fall, suggesting that, if insecticide treatments were warranted, they could be limited to this time period. Elsewhere, the time just before harvest is when peaches and nectarines are most susceptible to feeding damage, but could likewise be best protected by well timed insecticide applications (Grasselly *et al.* 1995).

## THRIPS MANAGEMENT IN GREENHOUSE ORNAMENTAL AND HORTICULTURAL CROPS

There are over 3.35 million ha of greenhouse production in China, most of which is devoted to horticultural crop production. The greenhouse industry is much smaller in the United States, and is largely devoted to ornamental crop production. A number of thrips species can be significant pests in greenhouse ornamental and vegetable crops. These include *Frankliniella intonsa* (Trybom), *F. occidentalis*, *H. haemorrhodalis*, *Echinothrips americanus* Morgan, *S. dorsalis*, *T. palmi*, and *T. tabaci*. Because of the diversity of species that

can occur in any particular greenhouse system, correct identification of species is critical to the success of a management program. In both China and the United States, blue and yellow sticky cards are used for monitoring thrips populations in greenhouses (Jacobson 1997; Ren *et al.* 2008). Blue cards are highly attractive to *F. occidentalis* (Brødsgaard 1989), but this color is not universally attractive to all thrips, and growers often use yellow sticky traps because these are attractive to other pests in addition to thrips (Jacobson 1997).

In greenhouse ornamental and horticultural crops, adult and larval feeding cause significant aesthetic damage to crops and is further exacerbated by virus transmission. Consumer demand for unblemished products has led to a near zero threshold for thrips in these crops, which contributes to intense insecticide use in many greenhouse production systems (Bethke and Cloyd 2009). Management is complicated because most greenhouses contain a diversity of crops (polycropped as opposed to most food crops that are grown in monoculture), and they are susceptible to a range of pests that must be managed simultaneously. Therefore, mixed applications of insecticides are often made to control multiple pests.

Alternative management tactics to the sole reliance on insecticides have been developed and are being deployed to some extent in greenhouse systems. Cultural controls for thrips management include reducing opportunities for thrips infestations from outside of the crops. These tactics include manipulating the greenhouse environment for management. Fine mesh screens to cover greenhouse openings such as vents help to exclude thrips, and elimination of weeds within and around houses to reduce source populations. Greenhouse covers that absorb ultraviolet (UV) light can deter thrips from entering greenhouses. The reduced UV light in the greenhouse environment disrupts host finding by thrips (Costa and Robb 1999; Antignus *et al.* 2001). There has been considerable interest in the use of trap plants in greenhouses to reduce thrips on a target crop. Research trials continue to show that these approaches can limit thrips abundance on target crops (Bennison 2002; Buitenhuis and Shipp 2006; Matsuura *et al.* 2006; Buitenhuis *et al.* 2007), and there is interest among growers for sustainable management practices. However, there must be a high value in using trap crops

to justify the additional cost for their maintenance and the loss of production space.

The proper use of biological control agents can improve management of thrips populations in greenhouses. Inundative releases of agents once populations have become established which will not prevent aesthetic injury so agents should be released inoculatively, beginning at crop initiation to also suppress thrips populations before they approach economically damaging levels. Several types of control agents are effective against thrips, and there has been interest in combinations of different biological control agents that would target different life stages. *O. insidiosus* prefers larval thrips but will readily prey on adults when available (Baez *et al.* 2004). Phytoseiid mites predominantly attack first instar thrips rather than larger life stages. One species that has generated a great deal of interest is *Amblyseius swirskii* (Athias-Henriot), which has recently become commercially available in Europe and North America. This phytoseiid species has proven to be a more effective thrips predator than two other commercially available species, *N. cucumeris* and *Amblyseius (Iphiseius) degenerans* Berlese. The soil dwelling *Hypoaspis* spp. that consume thrips pupae have also received considerable attention because of their ability to complement above ground predators of thrips and also contribute to management of other pests (Berndt *et al.* 2004).

Because of their value, a number of predatory species are available from commercial suppliers for thrips management. Considerable research effort has gone into improving the quality of mass produced biological control agents, and in making their production more economical through the use of factitious prey and artificial diets (Shapiro and Ferkovich 2002; Ferkovich and Shapiro 2004, 2007; de Clercq *et al.* 2005). More recent research has focused on improving the quality of mass produced predators during their shipment and their effectiveness at release. *Orius pumilio* (Champion) fed water or an aqueous sucrose solution during shipment (i.e., within 48 h before release) had higher initial predation rates upon release than when fed a protein diet (Shapiro *et al.* 2009).

In addition to improving the quality of mass produced biological control agents, the greenhouse environment can be altered to improve the activity and survivorship of biological control agents. For example,

survivorship and predation rates of the predatory mite *N. cucumeris* improve at low vapor pressure deficits (i.e., in a more humid atmosphere) (Shipp *et al.* 1996; Shipp and van Houten 1997). As an ancillary benefit, these conditions also favor infectivity of fungal pathogens, which can be effective biological controls against thrips (Shipp *et al.* 2003). Ugine *et al.* (2005a, b) in an efficient assay aimed at quantifying secondary acquisition of fungal conidia by second-instar western flower thrips showed that *Beauveria bassiana* (strain GHA) is highly effective at very low doses (LD<sub>50</sub> of 33-66 conidia/insect). In China, the work of Zhang *et al.* (2009) also showed that the invasive *F. occidentalis* is particularly sensitive to indigenous strains of *B. bassiana*. Recent developments portend well for the future use of mycopathogens in thrips management in greenhouse ornamentals and vegetables. As described above, commercial formulations of entomopathogenic fungi continue to be developed as biological control agents against thrips in greenhouse systems. Because these pathogens are relatively slow acting, applying them inoculatively when pest populations are low has been considered the most viable approach. Because the same strategy applies to arthropod predators, the effects of entomopathogens on beneficials continues to be a concern. Jacobson *et al.* (2001) found that commercial formulations of *Beauveria bassiana* are compatible with *N. cucumeris*, so that growers can benefit from both types of control agents. An additional concern with the use of fungal pathogens against thrips has been assuring proper deployment to where thrips are concentrated, such as flowers where *F. occidentalis* aggregates (Hansen *et al.* 2003). A novel approach to this has been to use other insects as carriers of fungal agents. Pollinators and predators, which are not highly susceptible to tested, commercial formulations of fungal pathogens, have been used successfully to distribute fungal pathogens in greenhouse crops for thrips management (Al-mazra'awi *et al.* 2006; Down *et al.* 2009). Further research is still needed to optimize these procedures.

## THRIPS MANAGEMENT IN OPEN FIELD FRUITING VEGETABLES

The diversity of open field grown vegetable crops that

thrips attack and the varying dynamics of thrips interactions with each crop mean that management programs must be adapted to each particular system. Crops such as pepper and eggplant can be managed differently than crops such as tomato because of the differing impact of natural enemies. In pepper and eggplant cropping systems, IPM programs based on conservation biological control can successfully manage thrips, even in the presence of *Tospoviruses*. As demonstrated in Florida and Japan, naturally occurring predators such as *Orius* spp. can rapidly colonize pepper and eggplant fields to suppress thrips populations and halt the spread of *Tospoviruses* (Nagai 1991; Ramachandran *et al.* 2001; Reitz *et al.* 2003). However, *Orius* spp. are highly susceptible to most classes of insecticides; therefore, care must be taken to avoid insecticides that will disrupt the predator (Reitz *et al.* 2003). Spinosyn-based insecticides (spinosad and spinetoram) are compatible with *Orius*-based IPM programs. These materials can be used to suppress pest thrips populations before predators have fully colonized a crop (Srivistava *et al.* 2008; Seal and Kumar 2010). Augmenting predator populations by planting attractive banker plants around field borders is a new promising management tactic (Bottenberg *et al.* 1999). Where *Tospoviruses* are a particular concern, planting pepper crops on ultraviolet reflective mulches is a viable tactic (Reitz *et al.* 2003). These materials suppress thrips populations by disrupting host finding by thrips. However, because of expense and the potential delay in crop maturity, ultraviolet reflective mulches may not be economically justified in all cases.

Tomato is an important vegetable crop that is highly susceptible to *Tospovirus* infection (Hanssen *et al.* 2010) and where thrips oviposition and feeding damage can reduce fruit quality (Salguero-Navas *et al.* 1991; Ghidui *et al.* 2006). Biological control from *Orius* spp. has not proven feasible because these predators, which would prey on adult thrips settling in tomato flowers, do not readily colonize tomato (Coll and Ridgway 1995; Baez *et al.* 2011); therefore, alternative tactics are necessary. A great deal of success has been made in integrated management approaches against *F. occidentalis* and TSWV in tomato, where the emphasis is on preventing the buildup of damaging thrips populations. Chief among tactics to effect this are the use of ultraviolet light reflective mulches, which re-

duces the ability of thrips to find plants (Stavisky *et al.* 2002), maintaining fertilization at optimal levels rather than overfertilization, which can attract western flower thrips (Brodbeck *et al.* 2001), and avoiding the use of synthetic pyrethroids, which induce western flower thrips populations (Funderburk 2009). As with other fruiting vegetables, ultraviolet reflective mulches significantly reduce thrips populations and disease incidence (Stavisky *et al.* 2002; Riley and Pappu 2004). The incidence of tomato spotted wilt can also be reduced by applications of acibenzolar-S-methyl, a compound that induces a plant's systemic acquired resistance responses (Csinos *et al.* 2001; Momol *et al.* 2004).

## THRIPS MANAGEMENT IN ONION

*Thrips tabaci* has historically been a major pest of onion, *Allium cepa* L., and related crops globally. Thrips feeding reduces photosynthesis, which ultimately reduces bulb size and marketable yield (Kendall and Capinera 1987; Fournier *et al.* 1995). More recently, the emergence of *Iris yellow spot virus*, which is vectored by *T. tabaci*, has led to an increased focus on managing *T. tabaci* (Gent *et al.* 2006). This virus has been detected in most onion producing areas of the world over the past 20 years, with yield losses in excess of 60% reported in some fields (Gent *et al.* 2006; Pappu *et al.* 2009). The emergence of IYSV highlights the dynamic, complex nature of thrips and *Tospovirus* problems at present. Isolates of IYSV in the state of Georgia in the southeastern US are more closely related to isolates from Peru than to isolates from the rest of the United States and infected plants in Georgia present different symptoms than found elsewhere in the US (Nischwitz *et al.* 2007). Because Peruvian onions are imported into Georgia, it is likely the virus was introduced from there, and possibly, a biologically distinct, more pestiferous biotype of *T. tabaci* has been introduced from Peru as well.

At present, there is still a heavy reliance on insecticides for management of *T. tabaci* in onion. Onion is a favorable host for *T. tabaci*, and colonization patterns indicate that most thrips within an onion field are progeny of relatively few *T. tabaci* immigrants (Mo *et al.* 2009). These predictable seasonal dynamics make it possible to better time insecticide applications to criti-

cal stages of population growth, especially early within the population growth phase. Nault and Shelton (2010) have proposed using action thresholds that are modified according to the efficacy of each particular insecticide. They recommend that the action thresholds should be directly correlated with efficacy, so that action thresholds would be lower for less efficacious insecticides. The development of robust action thresholds for any crop is a complex and challenging endeavor. However, this information will lead to improvements in the use of insecticides and insecticide resistance management, and ultimately reduce the number of insecticide applications that growers make (Hoffmann *et al.* 1995).

Alternative control tactics to insecticides for *T. tabaci* in onion tend to address cultural controls as no effective natural enemies are yet known in this agroecosystem. Host plant resistance to both *T. tabaci* and IYSV is being developed. Varieties that have yellow-green foliage tend to have lower thrips populations than do varieties with darker, blue green foliage (Diaz-Montano *et al.* 2010). Onions with more open architecture also have lower abundances of thrips, possibly because thrips are more exposed with this type of growth pattern (Coudriet *et al.* 1979). No onion germplasm with complete resistance to IYSV has been identified, but some cultivars have greater tolerance or lower susceptibility than others. Multani *et al.* (2009) recommend that late season assessments of IYSV severity be used to assess susceptibility rather than the initial time of symptom expression. If symptoms are not expressed until late yield loss may not occur. Increased plant density also seems to reduce the severity of IYSV. Straw mulch has also been shown to reduce thrips abundance in onion (Larentzaki *et al.* 2008). The application of straw mulch is a relatively inexpensive management tactic and reduces the risk of environmental contamination from insecticides.

## THRIPS MANAGEMENT IN GROUNDNUT (PEANUT)

Groundnut or peanut, *Arachis hypogaea* L., is a major agronomic crop in China and in the United States. It is grown throughout the southern US where an endemic

thrips *Frankliniella fusca* (Hinds) is a key pest (Culbreath *et al.* 2003). The most significant damage it creates in these crops is from the transmission of *Tomato spotted wilt virus* (Sakimura 1963), consequently, a great deal of research has been conducted on its management. One product of this research has been the development of a risk assessment tool for growers to use in planning groundnut crops, which highlights the importance of integrating available control tactics in a unified manner (Brown *et al.* 2007). As research continues, additional factors are built into this risk index to further refine it (Wells *et al.* 2002; Olatinwo *et al.* 2008). The primary management tactic for groundnut growers under this index is to plant TSWV resistant varieties. Further enhancing the effect of host plant resistance is delaying planting until when conditions are less favorable for disease development. In the southeastern US, delaying planting until mid or late-May significantly reduces the incidence of TSWV (Hurt *et al.* 2005). The underlying mechanism appears to be related to the natural seasonal declines in thrips abundance (Funderburk *et al.* 2002).

These seasonal declines appear to be triggered by naturally-occurring biological control agents. One of these key natural enemies of *F. fusca* in the groundnut system is the parasitic nematode *Thripinema fuscum* Tipping & Nguyen (Allantonematidae) (Tipping *et al.* 1998). Parasitism by this nematode ultimately renders females sterile (Sims *et al.* 2005) and alters feeding behavior so that viruliferous individuals are not as efficient transmitters of TSWV as their unparasitized counterparts (Sims *et al.* 2009). Consequently, *T. fuscum* is a valuable biological control agent against *F. fusca* in groundnut fields, with high levels of parasitism quickly followed by collapses in *F. fusca* populations and suppression in the spread of tomato spotted wilt (Funderburk *et al.* 2002). Developing techniques for augmentative releases of nematodes could further suppress disease spread by *F. fusca*. An *in vivo* system has been developed for production of another species, *T. nicklewoodi* (Siddiqi), which is an obligate parasite of *F. occidentalis* (Arthurs and Heinz 2002). Although many technical challenges remain, the fact that *Thripinema* naturally persist on plants in agroecosystems makes them amenable for use in inoculative or augmentative biological control programs.

Although *F. fusca* is present in Japan, it is not thought to occur elsewhere in Asia (Shiro Nakao, personal communication). Other pest species, in particular *T. palmi*, which vector *Groundnut bud necrosis virus*, and *S. dorsalis*, which vectors *Groundnut ringspot virus*, *Peanut chlorotic fanspot virus*, and *Peanut yellow spot virus*, in addition to *Groundnut bud necrosis virus* (Whitfield *et al.* 2005).

## THRIPS MANAGEMENT IN COTTON

Cotton offers a contrast to the issue of thrips in a cropping system. Thrips can be important pests of cotton in many regions of the world, but in certain circumstances thrips may be beneficial in cotton. In the United States, early season thrips populations can severely damage seedling cotton. Feeding damage at this stage reduces plant growth and vigor, ultimately reduce yield. Insecticides are commonly used to manage thrips populations at the seedling stage of crop growth because natural enemy populations are not sufficient for control at this time (Greenberg *et al.* 2009). There has been a recent transition from in furrow applications of carbamates and organophosphate insecticides to using seed treatments of neonicotinoid insecticides. These systemic insecticides can provide relatively long protection and therefore reduce overall insecticide use in cotton. Alternative management tactics that show utility include conservation, strip tillage, which reduces thrips abundance in addition to other agronomic benefits (Toews *et al.* 2010).

Historically, thrips have not been considered pests when cotton is mature. Recently though, *Frankliniella* flower thrips have been implicated in spreading *Fusarium verticillioides* (Saccardo) Nirenberg, a fungal pathogen that is associated with the emerging problem of hardlock of cotton in the humid southeastern United States (Mailhot *et al.* 2007b; Srivastava *et al.* 2010). In hardlock, the cotton fibers fail to expand after the boll opens. It is thought that thrips enter cotton flowers and passively introduce inoculum. Perhaps more important, thrips feeding damage creates greater opportunities for *F. verticillioides* conidia to penetrate the plant (Mailhot *et al.* 2007b). Suppressing thrips populations in flowering cotton reduces the incidence of hardlock and can lead to higher yields. *O. insidiosus*

can colonize cotton flowers closely tracks thrips populations in cotton flowers (Mailhot *et al.* 2007a). Therefore, it may be possible to properly conserve and augment populations of *O. insidiosus* to help suppress thrips in cotton flowers. In arid climates such as California and Australia, thrips may be beneficial as predators of spider mites (Trichilo and Leigh 1986; Wilson *et al.* 1996). This dichotomy of thrips acting as pests and beneficials points to the complexity of thrips ecology.

## CONCLUSION

It is evident that China and the United States are at risk for the development of new problems from thrips and thrips-transmitted pathogens. The risk is from the biology of thrips and the nature of modern agricultural and trade practices. It is interesting to note that three of the major global thrips pests, *F. occidentalis*, *S. dorsalis*, and *T. palmi*, have only recently emerged as significant pests. Their polyphagy certainly predisposes them to pests of numerous crops. Their spread around the world has been promoted by the increasing worldwide exchange of agricultural commodities (Morse and Hoddle 2006). Numerous other species share the polyphagous habits of these species, and some are important pests on more regionalized scales (e.g., *Ceratothripoides claratris*, *F. fusca*, *F. intonsa*, *F. schultzei*, *F. zucchini*, *Megalurothrips sjostedti*, *Thrips flavus*, *T. hawaiiensis*, *T. imaginis*, *T. obscuratus*, *T. parvispinus*, *T. setosus*), but could emerge as major international pests in the future. Other species, such as *F. tritici*, that are not considered as serious pests in their native ranges could become serious should they become invasive in new geographic regions.

As thrips continue to be spread internationally, there is a critical need for more information on their basic taxonomy, biology and ecology to better understand and manage them. As Mound (2005) eloquently stated, researchers involved with Thysanoptera have often been too narrow in their outlook. The lack of taxonomic expertise often leads to delays in the proper identification of newly invasive species, thus hindering opportunities for their management (Mound and Collins 2000). In turn, taxonomists must appreciate phylogenetic relationships within the Thysanoptera, and appreciate the intraspecific and interspecific variation, including spa-



tial and temporal population dynamics, that ecologists have recorded. Virologists as well must appreciate that thrips are not merely “flying hypodermic syringes” (Mound 2005) but that acquisition and transmission of *Tospoviruses* are contingent on unique biological attributes of thrips, including potential cryptic species, host plants and the pathogens, and their interactions (van de Wetering *et al.* 1998; Adkins 2000; Moritz *et al.* 2004a). Management programs developed by economic entomologists have historically been reactive in terms of how to suppress economically damaging thrips populations rather than proactive in understanding ecological factors that could regulate populations below economically damaging levels and avoid pest situations from arising (Stern *et al.* 1959).

There has been a recent trend towards focusing on management of thrips populations at economically acceptable levels rather than on complete control (Bielza 2008; Funderburk 2009). This trend is perhaps been born out of necessity more than philosophy because of the limitations of insecticidal control programs, and the need to conserve the limited number of effective insecticides through insecticide resistance management programs. Consequently, this has led to the development more holistic integrated approaches to crop management. A major step will be to ensure that management programs are cost effective and easy for growers to implement.

The major global thrips pests, including *F. occidentalis*, *S. dorsalis*, *T. palmi*, and *T. tabaci*, are among the best known examples of invasive species in the world. Their global spread means that similar pest problems will continue to be shared among countries and heightens the need for international collaboration to facilitate the management of these pests. We expect that collaboration between China and the United States on new management methods invasive thrips will greatly improve in the near future. As more collaborative projects are developed and established, the management of invasive thrips that are native to China or North America, or are invasive in both will improve.

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