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BIOLOGY AND ECOLOGY OF THE WESTERN FLOWER THRIPS (THYSANOPTERA: THRIPIDAE): THE MAKING OF A PEST

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ABSTRACT

In the past 30 years, western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), has become one of the most important agricultural pests worldwide. Certain biological attributes of this insect predispose it to be a direct pest across a wide range of crops. In addition to the direct damage it can cause, this species is an efficient vector of *Tomato spotted wilt virus* and other *Tospoviruses.* This review addresses questions regarding the biological and ecological attributes of western flower thrips that have enabled it to become a significant pest and make it so difficult to manage. These important life history traits include western flower thrips polyphagy and a tendency to reside and feed in concealed areas of flowers and fruits. Consequently, large populations can develop and disperse into a wide range of crops. The larvae and adults feed in a similar manner and can share the same host plant resources. The relatively short generation time and haplodiploid sex determination also contribute to the pest status of this species. These life history traits interact in complex ways to make western flower thrips one of the most significant and difficult to manage pests in the world.

Key Words: *Frankliniella occidentalis*, *Tospovirus*, behavioral ecology, pest status

RESUMEN

En los pasados 30 años, el trips occidental de las flores, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), se ha convertido en una de las plagas mas importantes de la agricultura mundial. Ciertos atributos biológicos de este insecto lo predispone para ser una plaga directa por un rango amplio de cultivos. Además del daño directo que causa, esta especie es un vector eficiente del *virus de la marchitez manchada del tomate*y otros *Tospovirus.* Este resumen se dirije a las preguntas sobre los atributos biológicos y ecológicos del trips occidental de las flores que le han permitido llegar a ser una plaga significante y hacerla tan difícil de controlar. Estas importantes características de su historia de vida incluyen la polifagia del trips occidental de las flores y su tendencia para morar y alimentarse en áreas ocultas de flores y frutos. Por consiguiente, grandes poblaciones pueden desarrollarse y dispersarse en un rango amplio de cultivos. Las larvas y adultos se alimentan en una manera similar y pueden compartir los recursos de la misma planta. El periodo de generación relativamente corto y la determinación haplodiploide de los sexos también contribuyen al estatus de plaga de esta especie. Estas características de su ciclo de vida se relacionan de una manera compleja para hacer que el trips occidental de las flores sea una de las plagas más significantes y difíciles para manejar en el mundo.

Over the past 30 years, western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), has become one of the most important agricultural pests worldwide. It is arguably the most studied thrips in the world today. The increasing importance of western flower thrips is clearly reflected by the increasing number of publications on this species relative to the proportion of publications on all Thysanoptera (Fig. 1). There are over 5,000 species of thrips, yet western flower thrips alone has accounted for one third of the publications on all Thysanoptera in the past 30 years.

This increasing interest in western flower thrips is a result of its significance as an agricultural pest, which raises the question of what has enabled it to become such a pest. Its pest status can be attributed to several factors, including its reproductive potential, invasiveness, range of host crops, ability to transmit plant viruses, and insecticide resistance. All of these factors are interrelated, and all are related to the basic life cycle and life history strategy of the species. This review addresses the biological and ecological attributes of western flower thrips that have enabled it to become a significant, difficult to manage pest. Many other species of Thripidae share these attributes of western flower thrips and therefore could emerge as significant pests.

Biology of Western Flower Thrips

The general life cycle of western flower thrips is similar to that of other species in the family Thripidae, consisting of an egg, 2 active feeding larval instars, 2 relatively quiescent pupal in-

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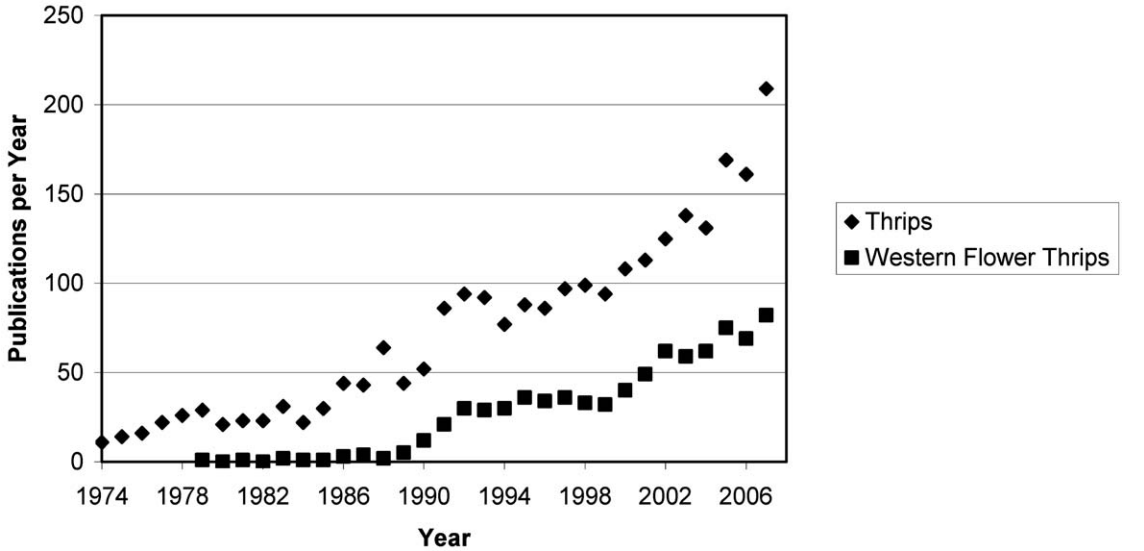

Fig. 1. Trends in the number of peer-reviewed journal publications on thrips in general and the western flower thrips in particular since 1974. Data are derived from searching the Web of Science® (http://apps.isiknowledge.com). A search for publications with the topic "thrips" or "Thysanoptera" was conducted to find publications on thrips in general. A second search for publications with the topic "*Frankliniella occidentalis*" or "western flower thrips" was conducted to locate publications specifically addressing *F. occidentalis*.

stars, and the adult. Adults and larvae aggregate in flowers or other concealed areas on plants, such as developing fruits, foliage, and floral buds (Hansen et al. 2003). This preference for residing in tightly enclosed and concealed spaces of plants is termed thigmotactic behavior. Females have a saw-like ovipositor, which they use to deposit eggs into leaves, petioles, flower bracts and petals, and developing fruit.

Sex determination in the western flower thrips is through haplodiploidy. The haploid males are produced from unfertilized eggs, whereas the diploid females are produced from fertilized eggs (arrhenotoky) (Moritz 1997). Although sex ratios of adults from field samples are often biased towards 1 sex or the other, mated females do not appear to allocate the sex of their progeny (Terry & Kelly 1993). Therefore, biases found in those adult sex ratios are likely a function of differences between the sexes in their dispersal, distribution in response to host quality, and longevity.

Development is temperature and host dependent but can be quite rapid, allowing multiple generations to occur in a single cropping season. Western flower thrips does not have an obligatory developmental or reproductive diapause (Ishida et al. 2003). Therefore, development occurs whenever temperatures exceed a minimum threshold of 8-10°C (Katayama 1997; McDonald et al. 1998). At the most favorable temperatures of 25-30°C, egg to adult development time can be as brief as 9-13 d (Lublinkhof & Foster 1977; Robb 1989; Gaum et al. 1994; Katayama 1997; Reitz 2008). The duration of the egg stage is relatively long, with hatching in 2-4 d at optimal temperatures. The first stadium is typically about half the length of the second (Gaum et al. 1994; Reitz 2008), after which feeding stops and pupation begins. Thrips often drop to the soil to pupate, but significant numbers can remain on host plants, especially if hosts have complex floral architecture (Broadbent et al. 2003; Buitenhuis & Shipp 2008). The first pupal instar is termed the propupa, a non-feeding stage that is followed by the pupa, another non-feeding pupal stage. Winged adults then emerge from the pupal stage in 1-3 d.

Under laboratory conditions, adult lifespan is relatively long compared with immature development time. For example, at 28°C, median egg to adult development time is 12 d, whereas median longevity for females is 26 d (Reitz 2008), with some females living up to 5 weeks (Trichilo & Leigh 1988; Hulshof & Vanninen 2002; Zhi et al. 2005; Reitz 2008). The relevance of these data to actual longevity in the field is unclear, but overlapping, continuous generations are likely to occur in the field. Although determining longevity in the field is problematic with such small vagile insects, mark-recapture studies indicate that adults can survive for over 5 d following release in pepper and tomato plantings (unpublished data).

Western flower thrips feed by piercing plant cells with their mouthparts and sucking out the contents (Hunter & Ullman 1989; Harrewijn et al. 1996). Adults and larvae feed in a similar manner, so both stages contribute to plant damage. In-

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dividuals tend to feed in localized 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). Western flower thrips also feeds on pollen (Trichilo & Leigh 1988), which can stimulate oviposition, reduce larval development time, and increase female fecundity (Hulshof & Vanninen 2002; Hulshof et al. 2003; Zhi et al. 2005; Riley et al. 2007). Although primarily phytophagous, adults and larvae will prey on spider mite eggs (Trichilo & Leigh 1986).

Western flower thrips fits the classic definition of an *r*-selected species (Pianka 1970; Reitz 2008). All studies of reproduction in western flower thrips have reported high fecundity for females. After an initial preoviposition period, a female can oviposit throughout her lifetime (Reitz 2008). With optimal temperatures and diets, females can produce up to 7 progeny per day and have average total lifetime fecundities exceeding 200 per female (Robb & Parrella 1991). This high level of fecundity leads to high intrinsic rates of population increase, so uncontrolled populations can multiply rapidly (Gaum et al. 1994; Gerin et al. 1994; Hulshof et al. 2003).

One of the most important aspects of western flower thrips biology is its polyphagy. This species is known to feed on over 250 different crop plants from more than 60 plant families (Robb 1989; Tommasini & Maini 1995; Lewis 1997). In addition, it occurs on many uncultivated plants (Chellemi et al. 1994; Paini et al. 2007). However, it is critical to distinguish between plant species that support successful reproduction and those on which adults feed but do not support successful breeding populations (Mound 2005). Paini et al. (2007) found that the range of adult feeding hosts in northern Florida is broader than the range of reproductive hosts, emphasizing the need to look beyond static records of plant associations to understand the ecology and population dynamics of western flower thrips. To avoid misunderstandings and misinterpretations, it is clear that the term "host plant" must be applied in the proper context.

Because of its polyphagous feeding and breeding behavior, western flower thrips is exposed to a broad diversity of plant allelochemicals (Feyereisen 1999). Therefore, it must be able to metabolize a broad range of allelochemicals, as well as produce inducible enzymes in response to specific compounds (Li et al. 2007). Unfortunately, there is little basic ecophysiology information on the response of western flower thrips to host plant chemistry. Based on pesticide resistance studies, western flower thrips has various metabolic detoxification enzyme systems that could help it to overcome secondary plant defenses (Jensen 2000; Espinosa et al. 2005). Chief among these systems are cytochrome P-450 monooxygenases, esterases, and glutathione *S*-transferases. Apparently, this generalist herbivore has many allelochemical-metabolizing genes to enable it to cope with the diversity of allelochemicals that it is likely to encounter (Li et al. 2007).

Western Flower Thrips as a Pest

Beginning in the late 1970s, western flower thrips began to spread widely from its native range in western North America (Kirk & Terry 2003). The exact cause for its spread is uncertain but increased global trade in floricultural and horticultural products has been implicated. A highly insecticide resistant strain originated in California as a result of intensive insecticide use in greenhouse crops in the 1970s and 1980s (Robb 1989; Immaraju et al. 1992). Western flower thrips is now established throughout North America, and many countries of Europe, Asia, South America, Africa, and Australia (Kirk & Terry 2003).

Whereas human assisted movement is undoubtedly responsible for many of the introductions of western flower thrips to new geographic areas, this species is also able to spread by other means within new areas (Kirk & Terry 2003). Thrips can move long distances on wind currents (Mound 1983). Spread is further enhanced by polyphagy and the ability of small founder populations to succeed. Several biological factors make western flower thrips an ideal invasive species to be spread by human activity. The small size and thigmotactic behavior of larvae and adults make detection difficult. In addition, because eggs are deposited within plant tissue, they are even less readily detected, and are less susceptible to fumigation than are other life stages (MacDonald 1993; Janmaat et al. 2002; Simpson et al. 2007). The polyphagous nature of western flower thrips increases the number of crops on which it may be exported from a country, and then enhances the probability of introduced individuals finding suitable hosts in new areas (Morse & Hoddle 2006). The high fecundity of females makes it possible for small founder populations to become established and grow rapidly. Further, the haplodiploid sex determination leads to strong selection against deleterious alleles in the haploid males (Denholm et al. 1998). Consequently, some small founder populations may readily adapt to new environments and be relatively resistant to the detrimental effects of inbreeding (Schmid-Hempel et al. 2007). Also, because of their potentially long adult lifespan, rapid immature development rate, and haplodiploid sex determination, unmated founder females could produce male progeny initially and survive long enough to mate with those males, thus making introduced populations as small as one potentially viable (Immaraju et al. 1992).

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The sheer number of crops that western flower thrips attacks is astounding. It is a significant pest of virtually all crops, including fruiting vegetables, leafy vegetables, ornamentals, tree fruits, small fruits, and cotton (Lewis 1997). The range of crops damaged by western flower thrips is simply a reflection of its inherent polyphagy. Direct crop damage results from both feeding and oviposition (Childers 1997). In addition, high fecundity and reproduction on a broad range of hosts enables large numbers to disperse into crop fields from many sources. Consequently, attempting to manage the sources of thrips is virtually impossible. In many floral and horticultural crops, western flower thrips populations are virtually guaranteed to exceed the low to non-existent damage thresholds (Robb & Parrella 1991).

Adult and larval feeding causes considerable aesthetic damage to ornamental and fruiting crops (Parrella & Jones 1987). Extensive feeding can also result in flower and fruitlet abortion, which is a direct yield loss (Childers 1997). Because of their thigmotactic behavior, feeding damage is often inflicted on developing tissue, which then goes undetected until flowers or fruit mature (Welter et al. 1990; Pearsall 2000; Steiner & Goodwin 2005; Ghidiu et al. 2006). Not all crops damaged by western flower thrips are reproductive hosts for the species. Those that only serve as adult feeding hosts, for example tomato (Brodbeck et al. 2001), can still be adversely affected by adult feeding.

Further complicating management, western flower thrips feeding damage can be confused with damage caused by other pests or diseases (Steiner & Goodwin 2005). Such incorrect diagnoses may result from the small size and cryptic habits of western flower thrips and the fact that damage is not immediately apparent and associated with the causal organism. Unfortunately, misdiagnoses often lead to inappropriate pesticide application.

Female oviposition causes another type of damage to developing fruits. Females insert eggs under plant epidermis with their saw-like ovipositor. This wounding elicits a physiological wound response in some plants that produces spotting on fruits. Extensive spotting can lead to downgrading of quality in tomatoes (Salguero-Navas et al. 1991), grapes (Jensen 1973) and apple (Terry & De Grandi-Hoffman 1988), among other crops.

By far the greatest damage caused by western flower thrips is its ability to transmit *Tospoviruses. W*estern flower thrips is known to vector 5 *Tospovirus* species, 2 of which, *Tomato spotted wilt virus* (TSWV) and *Impatiens necrotic spot virus,* occur in the United States (Whitfield et al. 2005). Although accurate data are difficult to obtain, an estimate that TSWV alone causes over $1 billion in losses annually has been reported (Goldbach & Peters 1994).

Over 1,000 species of plants in 84 families are susceptible to TSWV (Parrella et al. 2003), giving it one of the broadest host ranges of any plant pathogen. In 2 ways, this broad host range is clearly related to the distribution of its main vector, western flower thrips. First, because western flower thrips can reproduce on many different plants, viruliferous adults arise from many different sources. Given the fecundity of western flower thrips, large numbers of viruliferous individuals can be present in the environment at any time. Further, different source plants can harbor various strains of the virus, which further complicates the development of effective disease management programs (Ullman et al. 2002). Second, susceptible crops do not need to be reproductive hosts for the thrips because adults retain and transmit the virus throughout their lives (Ullman et al. 1993) and can feed on a wider range of plants than they use for reproduction (Paini et al. 2007). For example, most tomato spotted wilt in field grown tomato is a result of primary spread of the pathogen from viruliferous adults dispersing into the fields (Puche et al. 1995). Tomato is a poor reproductive host for western flower thrips (Brodbeck et al. 2001; Reitz 2002). In fact, it may be possible for epidemics of tomato spotted wilt to be greater in less preferred hosts if viruliferous individuals are more likely to feed briefly, but long enough for transmission to occur, and then move from plant to plant (Reitz 2005). Western flower thrips has an intimate, complex relationship with these viruses. For a western flower thrips to transmit TSWV, it must acquire the virus as a larva, primarily as a first instar (Tsuda et al. 1996; van de Wetering et al. 1996). Western flower thrips may acquire TSWV as an adult, but such individuals do not become competent vectors (de Assis Filho et al. 2004). Second instars are physiologically capable of transmitting the virus (Wijkamp & Peters 1993), but as they do not readily move from plant to plant, transmission is essentially restricted to vagile adults. Transmission can occur quite rapidly, in as little as 5 min of feeding (Wijkamp et al. 1996). The short time needed for transmission contributes to the ineffectiveness of insecticides to limit the spread of TSWV.

Because of the severe threat posed by western flower thrips, there has been a heavy reliance on insecticides for its management. However, the thigmotactic nature of this species limits its direct exposure to insecticides. For open field crops, the numerous reproductive hosts, high fecundity and rapid generation time of western flower thrips result in a constant influx of new immigrants which even repeated insecticide applications cannot successfully control (Bauske 1998).

Perhaps the most important problem with insecticide use is the ability of western flower thrips to develop resistance to insecticides. The first reported insecticide failure against western flower

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thrips was in 1961 and, since then, there have been numerous documented cases of resistance to most classes of insecticides around the world (Jensen 2000). The extensive resistance found in California greenhouse populations (Immaraju et al. 1992) has been implicated as a contributing factor in the worldwide spread of western flower thrips (Kirk & Terry 2003).

The polyphagous nature of western flower thrips plays a key role in its ability to develop resistance to insecticides. Because it is a pest of many crops, populations are often under constant insecticide pressure, which increases selection for resistance. Enclosed greenhouse environments also place populations under intense selection for resistance because they provide constant exposure to insecticides and limit immigration of susceptible individuals (Robb & Parrella 1991; Immaraju et al. 1992; Denholm et al. 1998).

The haplodiploid sex determination system in western flower thrips greatly accelerates the evolution of insecticide resistance (Denholm et al. 1998). In haplodiploid species, resistance genes are exposed to selection from the outset in haploid males, regardless of whether resistance alleles are dominant or recessive. Thus, resistance alleles can become fixed much more rapidly than if western flower thrips were diploid. Not only can western flower thrips evolve resistance rapidly, resistance can persist over many generations in the absence of selection (Robb 1989; Brødsgaard 1994; Bielza et al. 2008b). Even more troubling for resistance management programs is recent evidence that resistance to certain insecticides (i.e., acrinathrin and spinosad) does not come with a fitness cost to western flower thrips (Bielza et al. 2008a). Consequently, resistance could evolve faster and be maintained in populations longer, which would greatly affect the development and viability of insecticide rotation schemes and resistance management programs. As a polyphagous herbivore, western flower thrips has evolved numerous metabolic detoxification pathways to contend with diverse plant allelochemicals that it encounters. These versatile enzymatic systems predispose it to be able to metabolize many insecticides (Jensen 2000) and often confer cross-resistance to other insecticides (Brødsgaard 1994; Espinosa et al. 2002). Metabolic detoxification enzymes such as cytochrome P450 monooxygenases, glutathione *S*-transferases, and esterases have been implicated as contributing to insecticide resistance in various western flower thrips populations (Jensen 2000). The major detoxification pathway appears to be through metabolism of toxicants by cytochrome P450 monooxygenases (Espinosa et al. 2005). These enzymes are known to confer resistance and cross-resistance to pyrethroids, organophosphates, and carbamates.

Western flower thrips is clearly a formidable pest because of the range of crops it attacks throughout the world, the ever increasing amount of damage caused by its feeding, oviposition and virus transmission, and the propensity with which it develops insecticide resistance. While much has been learned about this species and how to manage it (see the other papers in this symposium), there is a clear need to continue development of more economically and environmentally sustainable management strategies for this devastating pest. To better manage this species, a greater understanding is needed of its biological and ecological attributes especially its biology, ecology and population dynamics outside of cropping systems. As formidable a problem as the western flower thrips has become, other thrips with similar biological and ecological attributes exist and could, likewise, rapidly emerge as serious global pests (Kirk & Terry 2003). Thus, increased knowledge about western flower thrips will help to avoid or mitigate damage due to other pest thrips.

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