The pest and vector from the West: *Frankliniella occidentalis*

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Abstract: The western flower thrips, *Frankliniella occidentalis* (Pergande), has become a major worldwide pest of agriculture and horticulture. The history of its spread and the economic cost of damage are reviewed. An understanding of feeding behaviour and activity is very important because feeding is responsible for both the direct damage to crops and also the indirect damage from the transmission of plant viruses. Some other interesting aspects of the biology of the species, which are of applied relevance, are discussed: variation, genetics, and responses of flying adults to colours.

Introduction

The western flower thrips, *Frankliniella occidentalis* (Pergande), has become a major worldwide pest of agriculture and horticulture. Much research is now directed at integrated pest management of the species, but there are also many other fascinating aspects of its biology. This paper reviews the history of its spread and the economic cost of damage and then discusses some interesting topics that deserve more attention.

The literature on this species published up to 1988 was listed by Mantel (1989) and the status of the species, based on literature to 1992, has been reviewed by Tommasini and Maini (1995). There are also recent reviews of selected topics, such as the predators (Riudavets, 1995) and parasitoids (Loomans and van Lenteren, 1995).

History

The western flower thrips was first described in 1895 from specimens collected in California, USA, where it was recorded as plentiful (Pergande, 1895). The species was originally placed in the genus *Euthrips*, but in 1912 it was transferred to the newly erected genus *Frankliniella* (Karny, 1912). This genus is the second largest in the family Thripidae, with about 160 species, and is predominantly American, in that nearly all the species are native to America, although many also occur elsewhere (Nakahara, 1997). It contains many important agricultural pests in addition to *F. occidentalis*, for example *Frankliniella bispinosa*, *Frankliniella fusca*, *Frankliniella intonsa*, *Frankliniella parvula*, *Frankliniella schultzei* and *Frankliniella tritici* (Lewis, 1997, Appendix II), and these species are often polyphagous. For example, Lewis lists four of them as pests of crops in at least three different families, including cotton (Malvaceae), cowpea (Fabaceae) and tobacco (Solanaceae). The genus also dominates lists of thrips species that are virus vectors (Ullman *et al.*, 1997). The genus *Frankliniella* has produced some of the most important thrips pests and the western flower thrips is currently one of the most damaging of them.

However, the species has not always been a major worldwide pest. Bailey (1940) reviewed the injurious thrips of the USA and described the species as common in the far western states of the USA. Unfortunately, he did not specify the damage from *F. occidentalis*, but lumped it together with that from all the other *Frankliniella* species. In California, however, it was considered the most damaging thrips species overall because of the wide range of crops it damaged, although other thrips caused more damage to certain crops (Bailey, 1938). Surprisingly, in the major review of the species by Bryan and Smith (1956), the pest status is not even mentioned.

Before the 1970s, *F. occidentalis* was described as occurring west of about 100? latitude in the USA, from North Dakota to Texas, mainly west of the Rocky Mountains, northwards as far as Alaska, and south as far as Mexico City, with only rare accidental importation to glasshouses in the eastern states of the USA (Bryan and Smith, 1956; Stannard, 1968). It is highly unlikely that it was present at that time in the eastern states,

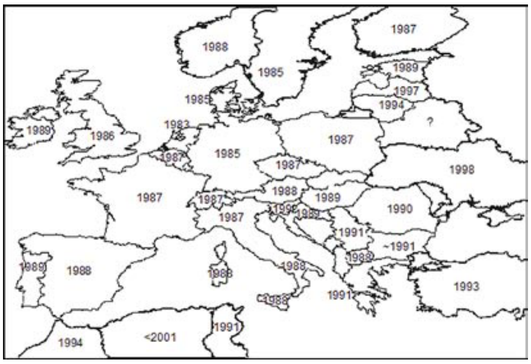

Figure 1. Map indicating the years in which the western flower thrips was first recorded. Data are from Tommasini and Maini (1995), with a correction for the UK (Baker et al., 1993) and additional records for Algeria (Schmid, pers. comm. 2001), Austria (Kahrer, 1989), Bulgaria (Donchev, 1995), Croatia (Simala, 1991), Czechoslovakia (Pelikan, 1989), Estonia (Luik, pers. comm. 2001), Latvia (Petrova et al., 2000), Lithuania (Ostrauskas, pers. comm. 2001), Macedonia (Andjus and Vukovic, 1991), Morocco (Hanafi, pers. comm. 2001), Romania (Vasiliu-Oromulu, 1993), Serbia (Andjus, 1992), Slovenia (Janezic, 1993), Tunisia (Zur Strassen, pers. comm. 2001), Turkey (Tunç and Göçmen, 1994), and the Ukraine (zur Strassen and Baranowski, pers. comm. 2001). For some countries there are no records or no data.

because if it were it would have been found and reported by Stannard in Illinois in the 1960s or Beshear in Georgia in the 1970s. The distribution of *F. occidentalis* in the far west of the USA contrasted curiously with that of *F. tritici*, which occurred in the central and eastern states of the USA (Bailey, 1940). Both were the dominant polyphagous flower thrips in their areas and were ecologically similar. The contrast in distribution was even reflected in their common names, since they were known as the western flower thrips and the eastern flower thrips (Stannard, 1968). If the distributions had shown a north-south difference, climatic differences might have been responsible, but both ranges included a wide range of climates, so it is difficult to understand what prevented the two species from spreading quickly across the width of the USA. One possibility is that inter-specific competition between the two abundant species has kept them apart and this would be well worth investigating.

There may also be competitive interactions affecting the distribution of other *Frankliniella* species. For example, the distribution of *Frankliniella minuta*, rather like the historical distribution of *F. occidentalis*, is restricted to the western states of the USA (Bailey, 1938; Nakahara, 1997). Old records show that *F. tritici*, despite being abundant in the eastern states, was replaced in the peninsula part of Florida by *F. bispinosa* (Watts, 1936), suggesting that *F. bispinosa* was excluding it. *F. tritici* is still extremely rare compared with *F. bispinosa* in citrus flowers in Florida (Childers, pers. comm. 2001). Such evidence from distributions and relative abundance suggests competition, but there are other possible explanations, and experiments are needed to test these hypotheses.

Examination of old collections has shown that *F. occidentalis* was also present in New Zealand, at least as far back as 1934 (Mound and Walker, 1982). It was particularly common on tree lupins (*Lupinus arboreus*) in sand dunes and caused no problems to crops. This biotype was therefore ecologically very different from that in the USA. Recent tests show it has low resistance to insecticides and it has been referred to as the lupin strain (Martin and Workman, 1994).

Although the distribution was apparently stable for decades in North America, something happened in the late 1970s and *F. occidentalis* started spreading. First it appeared in some eastern states of the USA, and then in the early 1980s it reached glasshouses in eastern Canada, where it caused severe epidemics of tomato spotted wilt virus (Broadbent *et al.*, 1987). Through the 1980s, it continued to spread quickly to nearly all the states of the USA and southern provinces of Canada.

In 1983, it was discovered in glasshouses in the Netherlands, and it then spread rapidly across the whole continent of Europe, usually in commercial glasshouses, but surviving and overwintering outdoors in warmer climates (Tommasini and Maini, 1995). A map of Europe with the years of first detection for each country shows a spread from the Netherlands focus across the whole of Europe and into northern Africa (Fig. 1).

Large amounts of damage were caused as the species spread, so it came rapidly to the notice of the plant health authorities in each country and detection records should therefore give reasonable estimates of actual arrival. Species identification of this non-European species was problematic at first. In the Netherlands, *F. occidentalis* was initially confused with *Frankliniella pallida* (Uzel) (Zur Strassen, 1986; Mantel, 1989), but the spread of associated damage shows that this was a real invasion and not a spread of species awareness for a species that was already present.

F. occidentalis was recorded for the first time in South Africa in 1987 (Giliomee, 1989) and in Australia in 1993 (Malipatil *et al.*, 1993). The species was already present in New Zealand, but in 1992 there were outbreaks in glasshouses of an insecticide-resistant strain, which suggested that a new biotype had arrived (Martin and Workman, 1994).

It is clear from the pattern of invasion of glasshouse crops that the thrips was spread in Europe by the trade in propagating material of glasshouse ornamentals (Baker *et al.*, 1993). This is not surprising as surveys of the international plant trade have found that 20% of cuttings and 12% of plants are now infested with *F. occidentalis* (Frey, 1993).

What caused *F. occidentalis* to change from being a regional polyphagous pest to a major worldwide pest? Understanding this could be very important as there are other regional polyphagous thrips that are ecologically similar and possibly waiting in the wings, such as *Frankliniella tritici* (Fitch) in the USA (Chellemi *et al.*, 1994), *Thrips imaginis* Bagnall in Australia (Kirk, 1987) and *Thrips obscuratus* (Crawford) in New Zealand (Mound and Walker, 1982). It has been suggested that a new insecticide-resistant biotype appeared in the 1970s that led to the rapid worldwide spread (Brødsgaard, 1989a, 1994; Robb *et al.*, 1995). Once a single large outbreak of an insecticide-resistant, polyphagous thrips has occurred in a large commercial glasshouse, the huge scale of the international trade in glasshouse ornamentals means that it could spread around the world very rapidly and standard quarantine and inspection procedures would be unlikely to be able to prevent it (Baker *et al.*, 1993). If so, initial selection for resistance outside glasshouses followed by a chance introduction to a commercial glasshouse that distributes plants widely could trigger a new worldwide pest. However, *F. occidentalis* also appears to have spread outdoors in the USA and it is perhaps less clear how insecticide resistance would have prompted this. It would imply that insecticides limited the range to western USA previously, which seems unlikely. If competition had restricted the range to the west, insecticide resistance might, however, have tipped the balance in its favour and allowed a spread. It would be useful to know to what extent *F. occidentalis* has spread outdoors on non-crops as well.

Species invasions present natural ecological experiments. Does the arrival of a new species decrease the abundance of other species or affect species composition? Glasshouses are highly artificial environments, so the effects may not be obvious there and would be difficult to interpret, but it would be interesting to compare outdoor thrips communities before and after the arrival of *F. occidentalis*. In Turkey, the arrival of *F. occidentalis* appears to have upset the thrips species composition on almost every crop on which it breeds (Tunç, 1999). In the USA, although *F. occidentalis* has spread to the eastern states, it has remained infrequent compared to *F. bispinosa* in citrus flowers in Florida, even though *F. occidentalis* is abundant and clearly does well in citrus flowers in Morocco (Childers, pers. comm. 2001). This situation mirrors the apparent long-standing exclusion of *F. tritici* in citrus flowers in Florida (see above).

There may also have been less obvious ecological consequences of the spread of *F. occidentalis*. Until the late 1980s, *Thrips tabaci* was a major vector of TSWV and thus caused major crop damage, but now many populations do not transmit tospoviruses and it has been suggested that virus isolates associated with *F. occidentalis* have displaced those associated with *T. tabaci* (Ullman *et al.*, 1997). If this is so, the change in relative abundance of the two thrips species has produced competition between tospovirus isolates, causing the virus to change its vector.

As *F. occidentalis* spread round the world, causing damage, it generated considerable research activity. It was probably the most researched thrips species of the twentieth century.

Damage	**Annual cost/loss**	**Region**	**Year**	**Reference**
Glasshouse crops - excluding TSWV	€ 34m $ 30m (Dfl 74m)	Netherlands	1998	(Roosjen *et al.*, 1998)
Glasshouse crops - TSWV	€ 21m $ 19m (Dfl 46m)	Netherlands	1998	(Roosjen *et al.*, 1998)
Direct loss of ornamentals	€ 20m-40m $ 18m-36m (£ 12.5m-25m)	UK	1999?	(Sampson, 2000)
All crops - thrips and TSWV	€ >6m $ >5m	Canary Islands	1989	(Pena Estevez, 1990)
TSWV	€ >0.75m $ >0.68m	Pennsylvania, USA	1989-1990	(Hausbeck *et al.*, 1992)
Glasshouse crops (actual)	€ 0.25m $ 0.23m (FIM 1.5m)	Finland	1988	(Rautapää, 1992)
Glasshouse crops (predicted if no initial eradication)	€ 1.5m $ 1.3m (FIM 8.9m)	Finland	1988	(Rautapää, 1992)
INSV on exacum	€ 0.17m $ 0.15m	one grower, east coast, USA	1995	(Daughtrey *et al.*, 1997)
INSV on imapatiens plugs	€ 0.17m $ 0.15m	one grower, New York, USA	1999	(Daughtrey, pers. comm., 2001)
INSV on ranunculus	€ 0.07m $ 0.06m	one grower, west coast, USA	1995	(Daughtrey *et al.*, 1997)
TSWV on chrysanthemums	€ 0.08m $ >0.07m (£ >0.05m)	one grower, UK	1989	(Baker *et al.*, 1993)

Table 1. Costs/losses resulting from the western flower thrips. These may be direct losses from damage, the cost of stock destroyed by plant health authorities, compensation or treatment costs. The costs are converted into euros and US dollars at the rates in 2001. The cost in the original currency is given in brackets.

Economic costs

A vast amount of crop damage has been caused by *F. occidentalis* in the last couple of decades. However, systematic national or regional records of total damage are not kept and research publications rarely state the financial costs of damage, so detailed figures for the amount of damage are hard to obtain. Growers are, understandably, reluctant to publicise that they have a thrips problem or that they have incurred a large loss. The situation can often be complicated by the presence of other pest thrips, such as *Thrips palmi*, or the presence of other species that might also be virus vectors. Costs and losses are difficult to compare because of the many ways in which they can be calculated, for example some losses give wholesale value and others give retail value. Some of the most detailed information comes from the Netherlands, where a model has been developed to estimate the annual national cost of damage from quarantine organisms in glasshouses, and this includes a fully broken down estimate of the cost of *F. occidentalis* (Roosjen *et al.*, 1998). Table 1 lists this and some other financial costs/losses resulting from *F. occidentalis*. Reference should be made to the original sources to see how the costs/losses were calculated.

Feeding behaviour and activity

An understanding of feeding behaviour is very important because feeding is responsible for both the direct damage to crops and also the indirect damage from the transmission of plant viruses. Diet is strongly linked with survival, growth and oviposition, so feeding behaviour can rapidly affect population dynamics. For example, at least 76% of the variance in resistance of chrysanthemum cultivars to *F. occidentalis* is explained by larval performance on extracted leaf sap (De Jager *et al.*, 1995). We know quite a lot about the mechanics of feeding in thrips, although some parts of the process are still unclear (Kirk, 1997). In contrast, we know much less about feeding behaviour, such as the diel pattern of feeding and what influences it. Research on diel patterns of movement, feeding and oviposition are in progress at Keele University. Differences in feeding behaviour between adult males and females affect tospovirus transmission (van de Wetering *et al.*, 1998), and further studies of differences in feeding activity between instars and sexes would be interesting. Sugar and yeast appear to be feeding stimulants (Brownbridge *et al.*, 2000), but it is difficult to test whether substances are feeding stimulants or deterrents because it is not easy to measure feeding activity directly. Although it is relatively easy to compare survival or growth between diets, these are confounded with other factors. Many thrips have mixed diets and little is known about the relative amounts of each food that are consumed when there is a choice (Kirk, 1995). Recent studies have shown that *F. occidentalis* reduces the amount of leaf feeding by about 50% when mite eggs are available (Agrawal *et al.*, 1999), so the effects can be large.

Variation

Many *Frankliniella* species are variable in colour and structure and are hard to identify. *F. occidentalis* is particularly variable in colour and size and this has led to a large number of synonyms (Nakahara, 1997). For many years, paler forms were considered to be *F. occidentalis* and darker forms were considered to be *F. moultoni* Hood (Bryan and Smith, 1956). The species is also particularly hard to identify because there is no single character that distinguishes it (Mound and Marullo, 1996). The species boundary may be rather indistinct and there is plenty of scope here for further research.

Bryan and Smith (1956) divided the colour forms of the adult females, which intergraded with each other, into pale (white and yellow throughout, except for slight brown maculations on the abdominal tergites), intermediate (orange thorax and brown abdomen), and dark (brown throughout). The adult males are all pale and do not show the variation. Inbred lines of the pale and dark forms were reared and the subsequent well-replicated crosses showed clearly that there was a simple mendelian genetic component of colour. The female genotypes were described as DD (pale), Dd (intermediate) and dd (dark). The dark colour was described as a recessive character, but this terminology is incorrect. Heterozygous females were intermediate in colour, so both the pale and dark alleles show partial dominance and are not recessive. The letters D_1 and D_2 would be more appropriate then D and d. The thrips appear to have been reared at constant temperature, although the temperature is unfortunately not specified in the paper and there are hints that the colour forms may have been reared at different temperatures (15°C, 20°C and 26.7°C). This means that the possible effect of variation in temperature was not investigated and could have been confounded with genotype; the rearing temperature could well affect the adult colour and interact with genotype. In addition, there may be differential survival of colour forms with temperature. The proportion of colour forms changes with seasonal changes in temperature (Bryan and Smith, 1956) and also varies with altitude (Mound, pers. comm. 2001). The situation may be complicated and deserves further study. Experiments on heterogeneous field populations in California might well give different results from inbred population in glasshouses.

The predominant form of the adult female in commercial glasshouses is yellowish orange with brown markings on the tergites, which appears to correspond with the intermediate form of Bryan and Smith (1956). However, the intermediate form would not breed true and would generate dark forms. Intermediate females (Dd) would have male progeny with the haploid genotypes D and d. Crosses of intermediate females with a mixture of D and d males would give a mixture of pale, intermediate and dark females. This does not fit the observation that dark females are extremely rare in commercial glasshouses (Brødsgaard, 1989a). Clearly, the situation is more complicated than the findings of Bryan and Smith (1956) suggest. It might be wise for authors to state which colour forms of *F. occidentalis* are used in experiments and to record the rearing temperature, just in case more than one species is involved or the forms behave differently.

Some doubt might be cast on the findings of Bryan and Smith (1956), but the rearing of inbred lines of the dark and light forms was repeated successfully by Sakimura (1962). It is worth noting that in both cases, dark and light forms were probably obtained from different places, rather than co-existing colour forms in the same place. Also, the rearing temperatures are not specified and it is unclear from the two papers whether the colour forms were reared at the same or different temperatures.

The colour forms show a correlation with body size and their frequency is affected by seasonal weather conditions. Pale forms are smaller and commoner after warmer weather, whereas dark forms are larger and commoner after colder weather (Bryan and Smith, 1956). An effect of temperature on colour form has been demonstrated in *T. tabaci* by Loomans (1997), who found that pale females became darker in one generation when moved from 25ºC to 20ºC and lighter in one generation when moved back. The presence of dark forms in field populations in California and the virtual absence of dark forms in *F. occidentalis* in European glasshouses is, as yet, unexplained.

The colour forms of *F. schultzei* differ in their transmission of tospoviruses (Wijkamp *et al.*, 1995), but studies of the colour forms of *F. occidentalis* showed similar transmission efficiencies (Sakimura, 1962). It would be worth retesting *F. occidentalis* with modern tospovirus isolates once the colour variation is better understood.

During the spread of the western flower thrips across Europe, repeated genetic bottlenecks when small numbers of individuals established new colonies would be expected to have reduced genetic variation. Molecular studies with RAPD-PCR have been unable to separate stocks from Europe and Australia into biotypes (Ready, 1998). However, direct tests on stocks have shown clear differences in insecticide resistance (Brødsgaard, 1994), amount of leaf damage, reproductive rate and adult survival (de Kogel *et al.*, 1998).

Responses to colours

Brødsgaard (1989) compared 20 colours of vertical sticky trap in whitewashed glasshouses in Denmark and found that one tint of blue (Riacryl 257) stood out as the most attractive colour for *F. occidentalis*. Riacryl 257 is light blue, resembling colour number 279 in Pantone colour charts. It has low reflectance at 350nm (i.e. low UV), a broad peak at about 440nm, low reflectance at 600nm and another peak at 750nm. It looks rather like the colour of the sky, but it lacks UV, so would not look like the sky to a western flower thrips.

A comparison of 84 colours of vertical sticky trap in non-whitewashed glasshouses in Canada also found that a tint of blue (BT4) gave the highest trap catch (Vernon and Gillespie, 1990). It was also a slightly desaturated blue (i.e. a little white was added) with low UV, and had low reflectance at 350nm, a peak at about 450nm and low reflectance at 600nm. The reflectance beyond 650nm was not measured, but longer wavelengths are irrelevant as spectral efficiency curves indicate that the western flower thrips does not see beyond about 650nm (Matteson *et al.*, 1992). Blue tints that were slightly less or more desaturated caught significantly fewer thrips.

These results were surprising because yellow, not blue, tends to be most attractive to phytophagous insects, although flower-dwelling insects are often different (Kirk, 1984). They were also surprising because the response was specific to just one tint of blue. A response to one particular tint might be useful in a monophagous insect where the tint matched its hostplant, but *F. occidentalis* is highly polyphagous, so the response appears redundant for host-finding. The optimal blue tint attracts females and males, but the ratio of females to males was consistently higher on blue than on yellow or white with low UV (Vernon and Gillespie, 1990). This differentially high attraction of females suggests a host-finding role.

The blue response may affect host specificity. Brødsgaard (1989) observed that more thrips were present in light blue cultivars of *Saintpaulia*, which had a strong peak at 450nm, than in dark blue cultivars, and Robb (1989) found significant correlations between flower reflectance at 475nm and the number of thrips in flowers when compared between cultivars of rose or cultivars of carnation. However, there is no evidence that this is adaptive; comparisons of thrips performance between cultivars of miniature rose found other colours were better (Bergh and Le Blanc, 1997). Other species, such as *Megalurothrips usitatus* (Chang, 1990), *Thrips hawaiiensis* (Chiu and Wu, 1993) and *T. palmi* (Brødsgaard, 1989b) also appear to be attracted to particular tints of blue, which suggests a more general response than specific host-finding. The evolutionary significance of the response to one tint of blue remains unclear.

F. occidentalis appears to be a dichromat, with two peaks (λ_{max}) of spectral sensitivity, at UV (about 365nm) and green (540nm) (Matteson *et al.*, 1992; Walbank, 1996). However, the majority of insects are trichromats, with three peaks, at UV (about 350nm), blue (about 440nm) and green (about 530nm). This is though to be the primitive condition, and there is no obvious common adaptive cause for the loss of one receptor type among the few insects, such as the American cockroach and some ants, where this has occurred (Briscoe and Chittka, 2001). The wavelengths of the peaks for *F. occidentalis* do not match the peaks in the preferred tint of blue, but this would not be expected. Preferences only require changes in the relative synaptic efficiency between neurons coding information from the receptors, and there are no convincing examples of adaptive tuning of photoreceptors for colour vision in insects (Briscoe and Chittka, 2001).

It is worth noting that the attractive colour is a very specific tint of blue and that some of the blue traps available commercially, which are rather variable, almost certainly do not exploit the maximum response. Some may be no better than yellow traps. Trapping experiments in which an arbitrary blue is used are also liable to miss the maximum response and may misleadingly conclude that other colours are better than blue.

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