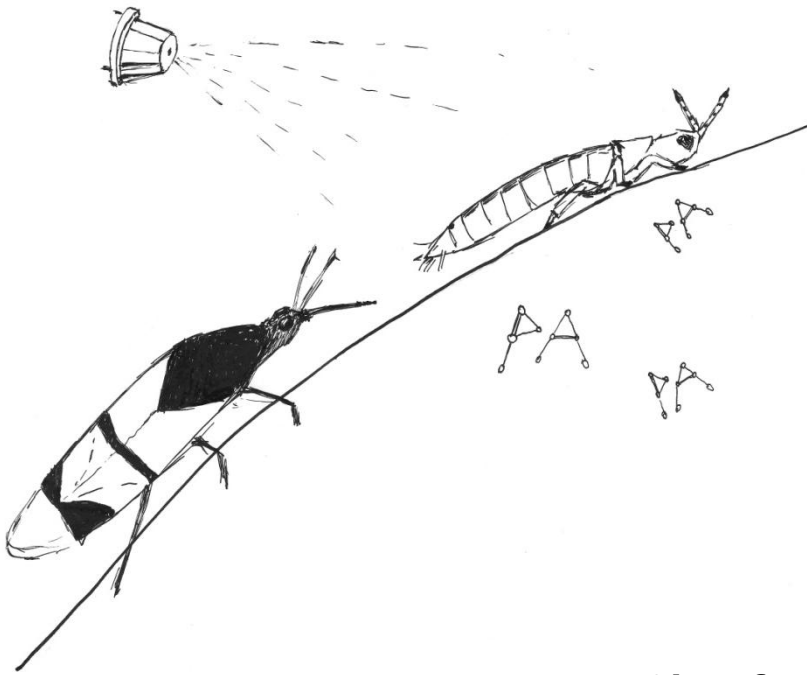


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Integrated Pest Management of Western Flower Thrips



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Abstract

Western flower thrips (WFT), *Frankliniella occidentalis*, is one of the most serious pests in agri- and horticulture worldwide. It is a highly polyphagous insect causing direct damage by feeding on plant parts such as foliage and flowers. In addition, it is a major vector for several plant viruses which leads to indirect damage. IPM programme for *F. occidentalis* already exist but has not led to full control of this pest. The overuse of pesticides in ornamental crops due to low tolerance to damage and pests characteristics such as short generation time, high fecundity, and parthenogenesis has led to resistance development in *F. occidentalis*. Moreover, its thigmotactic and cryptic behaviour makes it hard to combat chemically. Strategies that are essential part of IPM are biological, chemical and cultural control. Biotechnological advancement has made it easier to detect resistant cultivars against *F. occidentalis*. Moreover, host plant resistance has shown promising use and can be combined with biological control to strengthen IPM. Chemicals are still unavoidable in the horticulture for example spinosad therefore alternative natural insecticide such as pyrethrins are being used. For biological control predatory mites, bugs and entomopathogens are used while for cultural control mechanical trapping and trap plants are used. In addition, plant volatiles are combined to use pull-push strategies and to increase the efficiency of mechanical practices. The best control would be to eventually use all tactics of IPM to combat *F. occidentalis* on all angles. Awareness and education on IPM are necessary to fill the gaps in knowledge. Improvement in techniques in identifying the pest and identifying resistance within cultivars will also help breeding programs. Furthermore, evaluations of the success of IPM need to be followed up.

“The truth I seek, but, alas, what truth might there be, I have yet to learn.” -A frequently quoted sentence by scientists (Hartmann et al., 2008)

1. Introduction

The cultivation of plants began around 9000 years ago as discovered by archaeologists (Scheffer, 1996). By domesticating plants and growing it at a large scale people were able to settle at one place and produce food and feed for cattle. This process was the beginning of agriculture, which to this day has grown exponentially to feed a growing world population (Scheffer, 1996). The beginning of large scale monocultures has resulted in the establishment of the leading modern day farming systems, comprising indoor glasshouses or large outdoor fields. In both systems pest problems developed that in a more natural setting did not exist. The domestication of wild plants has led to the selection of traits such as high yields and favourable taste. However, throughout the years phenotypic and genetic variations were reduced and as an effect the loss of resistance (Hull-Sanders and Eubanks, 2005; Leiss *et al.*, 2011). The growing demand by consumers and profitability of mass production has led to a decreased investment in biological knowledge. As a consequence the development and application of more easily applicable control methods such as the use of pesticides was preferred. Synthetic insecticides were developed and implemented around the 1940s-1960s (Kogan, 1998). Pests could initially be controlled but excessive use led to the development of pest resistance to most chemical groups of pesticides used (Gao *et al.*, 2012). Moreover, intensive use of insecticides has led to many risks such as development of resistance by the targeted pest (Gao *et al.*, 2012), secondary pest resurgence (Gao *et al.*, 2012; Jensen, 2000a; Li *et al.*, 2007), non-target effects, contamination of crops and the environment, and health effect to human (Mostafalou and Abdollahi, 2013). Non-target organisms such as bees and bumblebees have shown to be affected in a negative way by neonicotinoids (Whitehorn *et al.*, 2012). All these negative effects have led to new regulations regarding registration and application of pesticides by the European Union (Coelho, 2009; Leiss *et al.*, 2011). Moreover, increasing international trade has led to a rapid and vast spread of pests worldwide. Before, mass production crop cultivation has been protected from pests based on biological knowledge and cultural practices. A practice regarded as precursor to the modern day Integrated Pest Management (IPM) (Kogan, 1998). The commonly used definition is: “*Integrated Pest Control is a pest management system that, in the context of the associated environment and the population dynamics of the pest species, utilizes all suitable techniques and methods in as compatible a manner as possible and maintains the pest population at levels below those causing economic injury*” – Kogan (1998).

In IPM not only insects are considered to be pests but also weeds, pathogens (fungi, oomycete, bacteria and viruses), and non-arthropod organisms such as nematodes (Kogan, 1998). Here the focal point is on insect pest thrips species *Frankliniella occidentalis*.

One of the most notorious pests in both agri- and horticulture is Western Flower Thrips (WFT) (*Frankliniella occidentalis*). These thrips is such a problem due to its broad range of hosts, their small size, making them hard to detect, their cryptic and thigmotactic behaviour and their fast and high reproduction rate (Morse and Hoddle, 2006). Before the 1970s *F. occidentalis* occurred to be in the North-West of America and Mexico and while another thrips species *Frankliniella tritici* occurred East-Central of America (Kirk, 2002). The name gives the origin of spread of the species in America (Kirk and Terry, 2003) hence *F. occidentalis* is the western flower thrips and *F. tritici* the eastern flower thrips. After that *F. occidentalis* appeared in Canadian glasshouses in 1980s and had spread throughout America (Kirk and Terry, 2003).

F. occidentalis began spreading globally when the international trade in horticultural products expanded during the 1970s (Kirk and Terry, 2003). Before that time, *T. tabaci* has been known as a native pest ((Van Rijn *et al.*, 1995) and therein). However, *T. Tabaci* and was replaced by *F. occidentalis* around 1985 (Kirk, 2002). The first detection of *F. occidentalis* in Europe was in the Netherlands in 1983 (Vierbergen, 2001). In 1987 the first witness of *F. occidentalis* beyond Europe was in South Africa and then in 1993 in Australia ((Kirk, 2002) and therein). *F. occidentalis* also occurs in countries with hot climates such as southern Italy which was discovered to colonize wild plants surrounding crops and glasshouses (Marullo, 2001) or Australia (Schellhorn *et al.*, 2010). Moreover, it quickly invaded New Zealand, Japan, South Korea, Malaysia, and Cameron, African countries via plant material due to trade ((Perrings *et al.*, 2005) and therein). In China it had invaded in 2003 and became a major pest in roses and (Shan *et al.*, 2012). All of the above aspects make this pest a successful invader, rapidly spreading, and causing large economic damage worldwide (Kirk and Terry, 2003). Currently, the main method to control thrips is the use of insecticides. However, due to the problems of excessive insecticide use resistance within many thrips species have developed. For *F. occidentalis* resistance against various insecticides (e.g., pyrethroids, organophosphates and carbamates) have been discovered for the past two decades ((Gao *et al.*, 2012) and here within). Four possible mechanisms will be discussed and these are: 1) metabolic detoxification which is mostly recognized, 2) reduced penetration of chemicals, 3) alteration of target site and 4) behavioural resistance.

Firstly, *F. occidentalis* has a polyphagous feeding habit and just like other generalist herbivorous insects it inherited a great abundance and diversity of genes to detoxify a great array of plant material. These detoxifying genes mostly code for enzymes (Li *et al.*, 2007) and work by converting hydrophobic compounds into less biologically active ones (Jensen, 2000a). They belong to the following families: Cytochrome P450 monooxygenases (P450s), esterases and glutathione-S-transferases (GSTs) (Kostaropoulos *et al.*, 2001; Yu, 1996). In *F. occidentalis* detoxification by P450s is the major mechanism of resistance because of its catalytic versatility and broad substrate specificity (Feyereisen, 2005). They detoxify pyrethroids which modulate sodium channels (Espinosa *et al.*, 2005). Organophosphate (Zhao *et al.*, 1994) and carbamates (Jensen, 2000b) on the other hand inhibit acetylcholine esterase. The esterases as well as GSTs are also involved in resistance to the above named insecticides but through enhanced activity of these enzymes. Detoxifications by esterases, however, have a lesser role in resistance as shown in numerous studies (Jensen, 1998; Maymo *et al.*, 2002). Secondly, there is the mechanism of resistance whereby penetration of the toxicant is reduced, thereby enhancing other resistance mechanisms (Gao *et al.*, 2012). An example is the resistance of several populations of *F. occidentalis* to fenvalerate (Jensen, 2000b; Zhao *et al.*, 1995a). The third mechanism consists of insensitivity to insecticides due to knock down or mutation (Davies *et al.*, 2008; Forcioli *et al.*, 2002) of genes or due to change of the target site (Zhao *et al.*, 1994). An example of the knockdown resistance (*kdr*) is the mutation of leucine to phenylalanine. Forcioli *et al.* (2002) reported at least four different amino acids that are known to be linked to pyrethroid resistance. There are also two different modifications of acetylcholinesterase (AChE) that confer resistance to insecticides. One is the resistance to diazinon due to insensitivity of AChE (Zhao *et al.*, 1994) and the second one is the increased activity of AChE (Jensen, 1998). These correlated with resistant strains of *F. occidentalis* (Jensen, 1998; Zhao *et*

al., 1994). The last mechanism is not well studied and is called the behavioural resistance (Jensen, 2000a). This system relies on selection of individuals that survive insecticide sprays due to cryptic and thigmotactic behaviour. Population studies on *F. occidentalis* have indicated that this affects their life cycle and thus their strength in (Hulshof *et al.*, 2003; Zhang *et al.*, 2007) being invasive. Overall, not only one resistance mechanism plays a role in development of insecticide resistance and, therefore, insect pests can develop several different unrelated ways of insecticide resistance. As such *F. occidentalis* is polyfactorial meaning that different mechanisms can confer resistance in different populations and/or coexist in one population (Jensen, 2000a). For that reason, new ways of thrips control have to be developed.

Implementing an IPM program is important to combat *F. occidentalis* in many aspects and to reduce its rapid and vast spread in agriculture and horticulture. A review by Cloyd, (2009), focusing on the use of insecticides and their problems in WFT management indicated the importance of biological control as a long-term strategy to deal with WFT. Here, an overview of different *F. occidentalis* control strategies will be given with focus on host plant resistance and recent strategy developments.

To understand and develop IPM programmes for thrips control knowledge of *F. occidentalis* biology and damage is essential. In this review these two topics will be first addressed, before continuing with a description of the research and implementation of *F. occidentalis* management tactics including chemical -, biological- and cultural control as well as host plant resistance. Finally, we will discuss future chances and challenges for thrips IPM development.

2. Thrips

Thrips have become an economically important worldwide pest due to an intense increase and spread of plant commerce. One of the sources of thrips as a pest is the handbook of agricultural pests by Kono & Papp (1977). It identifies some common pests such as aphids, thrips, mites, snails and slugs. Thrips are minute insects of 0,5 to 5,0 mm in size. They belong to the order Thysanoptera, which contains about 5500 described species (Morse and Hoddle, 2006). Thysanoptera differ from other insect orders by their asymmetrical mouth parts whereby the left mandible is developed and the right mandible is vestigial. In addition, the order name indicates another distinct feature: “thysanos” the Greek word for fringe and “ptera” referring to wings (Tipping, 2008). They have two slender pairs of wings with few or no veins and a dense fringe of long hairs (Tipping, 2008). The order contains two suborders Terebrantia and Tubulifera. Female Terebrantia have saw-like ovipositors (Kono and Papp, 1977) to place their eggs within the tissue of the plant. On the other hand, female Tubulifera do not have ovipositors (Kono and Papp, 1977). Therefore, the last abdominal segments of terebrantians are short and pointed whilst the one of the tubuliferans are long and tubular (Tipping, 2008). The suborder Tubulifera contains only family Phlaeothripidae while the suborder Terebrantia contains eight families of which the family Thripidae mainly contains thrips genera that cause damage on crops (Morse and Hoddle, 2006). Most pests have been found in three genera, *Frankliniella*, *Scirtothrips*, and *Thrips*. The second largest group is *Frankliniella* spp. containing many agricultural pests that are often polyphagous (Kirk, 2002). As such the notorious crop pest *F. occidentalis* has a host range of about 327 plant species (Lewis, 1997). *F. occidentalis*

feed mainly on plant leaves and flowers (Morse and Hoddle, 2006), however, some even are predatory (Martini *et al.*, 2013) or feed on fungal spores (Morse and Hoddle, 2006).

The financial costs owing to *F. occidentalis* damage are hard to obtain because total damage is not available and in the literature seldom stated (Kirk, 2002). In a study by Roosjen *et al.* (1998) a calculation was made in a model of annual cost of damage of *F. occidentalis* in Dutch greenhouse vegetable and ornamental crops which has been estimated to be 55 million euro ((MacDonald *et al.*, 2002) and therein). *F. occidentalis* does not only damage plants directly but also indirectly resulting in major yield losses (Shipp *et al.*, 2000).

2.1 Biology of *Frankliniella occidentalis*

The full length of a female *F. occidentalis* is about 1,5 mm and that of a male about 1,0 mm (Steiner, 2004). In addition, they have many colour forms and similarities with other pestiferous thrips (Morse and Hoddle, 2006; Steiner, 2004). The female colour ranges from light yellow to yellow with brown blotches. The colour of the blotches ranges from brown to dark brown (Kono and Papp, 1977). In contrast to the females males are light yellow (Kono and Papp, 1977). Larvae are white or yellow in colour and are wingless (Steiner, 2004). The WFTs also have reddish-orange ocellar pigments (Steiner, 2004).

The life cycle of *F. occidentalis* consist of four developmental stages *Figure 1*: egg, two larval instars and two pupal instars namely prepupa and pupa and adult (Lewis, 1997). Depending on the thrips species and their food quality about 30 to 300 eggs are laid by the females (Lewis, 1997). Moreover, females oviposit throughout their life after the first oviposition (Reitz, 2009). The eggs are also large relative to the female body and smoothly shelled. The two larval instars are active feeders and the following two stages prepupa and pupa do not feed (Dreistadt *et al.*, Revised 2007; Robb and Parrella, 1991)(Dreistadt *et al.*, Revised 2007; Robb and Parrella, 1991). The first larval instar is not as active in feeding as the second larval instar (Reitz, 2009). The metamorphosis from the first to the second instar takes 1-3 days and is temperature dependent (EPPO, 1989). The switch to pupation can take place in the soil or within flower structures and this takes about 2-9 days again depending on the temperature (Nothnagl *et al.*, 2007). The life cycle from egg to adult of *F. occidentalis* can be as short as 9-13 days at favourable temperatures of 25-30°C (Reitz, 2009).

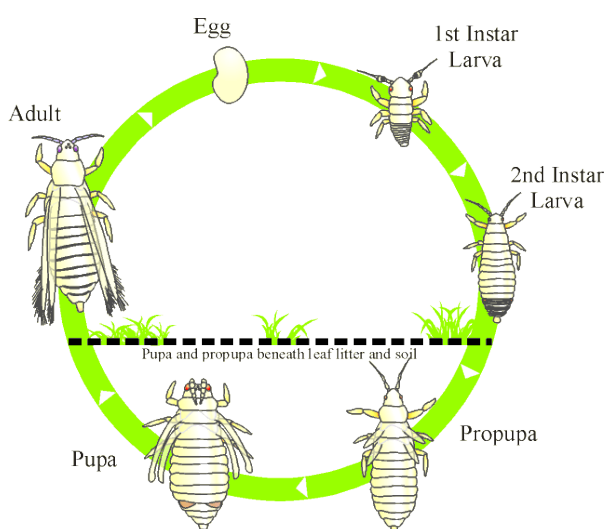


Figure 1 Thrips Life Cycle from <http://www.discoverlife.org/>
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F. occidentalis reproduces parthenogenetically by arrhenotoky whereby unfertilized eggs develop into haploid males and fertilized eggs turn into diploid females (Moritz *et al.*, 2004). After emergence adult females are somewhat inactive but after 24 hours they become extremely active. Under laboratory conditions, females live about 40 days but can survive as long as 90 days (EPPO, 1989). Males on the other hand live half as long as the females. *F.*

occidentalis has a fast reproductive rate not only because unfertilized eggs can develop into males but also because oviposition begins right after emergence and continues intermittently throughout almost all adult life. Furthermore, since females live longer than the respective males, they may switch from parthenogenesis to sexual reproduction by mating with their sons ((Nothnagl *et al.*, 2007) and therein). Both sexes also lack diapause making them present all year round in the crops (Morse and Hoddle, 2006; Steiner, 2004).

Problems concerning *Frankliniella occidentalis*

For the last 36 years *F. occidentalis* has been one of the most invasive insects and thus has developed into a worldwide pest (Kirk and Terry, 2003; Reitz *et al.*, 2011). There are many factors of its biology to why it is so troublesome. First they are very small insects of a few millimetres size and, therefore, hard to notice on site. Secondly, they are thigmotactic scurrying away from movements and they show a cryptic life style living in complex and obscure plant parts such as inside floral buds, folded tissues, within leaf bases and along leaf veins (McKellar *et al.*, 2005; Morse and Hoddle, 2006). Their eggs are deposited in sub-epidermal tissue of floral buds and leaves. This affinity for enclosed spaces makes it hard to control *F. occidentalis* with chemicals. Third, *F. occidentalis* is polyphagous meaning they feed on various kinds of plants. Within the cultivated plants thrips is a main pest in greenhouse agriculture and horticulture. Mainly vegetables such as cucurbits and peppers, (Dreistadt *et al.*, Revised 2007; EPPO, 1989) are host plants. For the ornamentals they are mainly roses and carnations in America (EPPO, 1989) and chrysanthemum in Europe (Van der Linden *et al.*, 2013). Lastly, *F. occidentalis* is difficult to identify, due to their small size and similarity with other thrips (Brunner *et al.*, 2002). In addition their high phenotypic plasticity for morphological traits makes determination even harder (Morse and Hoddle, 2006).

Damage

Direct damage is caused by the feeding behaviour of *F. occidentalis* on leaves and flowers ((Cloyd, 2009) and therein). This happens by puncturing holes with their piercing-sucking mouthparts. Thrips are cell feeders; they suck up the whole content of plant cells (Wetering *et al.*, 1998). Moreover, when mesophyll and epidermal cells are sucked up surrounding cells are damaged by the insertion of the stylet (Jensen, 2000b; Wetering *et al.*, 1998). Feeding on expanding tissue leads to local necrosis appearing as scars. The scarring is called “silvery appearance/damage” and is caused by air filling the empty cells (De Jager *et al.*, 1993; Wetering *et al.*, 1998). Scarring leads to a reduced photosynthesis capacity of the host plant causing reduced yields as well as a lower marketing quality in ornamentals due to cosmetic damage. Feeding on developing tissues leads to stunted and deformed plant growth causing malformation of flowers and fruits (Ullman *et al.*, 1989). In addition, leaves and flowers are also damaged when females deposit their eggs within the tissue using their curved ovipositors (Jensen, 2000a; Tipping, 2008). Indirect damage is caused by virus transmission. *F. occidentalis* are the vectors of several destructive plant viruses from the genus *Tospovirus* (Bunyaviridae) (Daughtrey *et al.*, 1997; Pappu *et al.*, 2009; Webster *et al.*, 2011). Examples are the Tomato Spotted Wilt Virus (TSWV) (Reitz, 2009; Stobbs *et al.*, 1992) and the Impatiens Necrotic Spot Virus (INSV) (Riley and Pappu, 2004).

Competitiveness

A study by Rijn et al. (1995) suggested that *F. occidentalis* is a superior competitor to *T. tabaci*. Even though there was no difference between the two species in the intrinsic rate of increase of net reproductive time and development time *F. occidentalis* still displaced *T. tabaci* from its pest status in Europe (Kirk, 2002; Morse and Hoddle, 2006). They had many hypotheses but few of the factors that indeed stand out are limited pesticides for *F. occidentalis* (Bielza et al., 2007a), their lack in diapause phase (McDonald et al., 1998) and the ability to prey on other herbivores (Funderburk et al., 2000). *F. occidentalis* was also competitively superior to *Frankliniella bispinosa* a thrips species common to southern Florida (Northfield, 2005). Recent findings suggested that interspecific competition from *F. bispinosa* does not limit the invasion of *F. occidentalis* but *F. bispinosa* still dominates the region (Northfield et al., 2011).

3. IPM

3.1. History of IPM

As stated in the introduction during the onset of agriculture man has adopted many methods in safeguarding their crops against pest. This was then termed “Pest control” and it constituted of actions to avoid, attenuate or delay pests from damaging their crops. Most control practices were mechanical such as weeding or cultural such as crop rotation. Before the discovery of synthetic chemicals in the early 1940s other compounds such as Bordeaux mixture, sulphur and lead arsenate were already used. The overreliance on insecticides had begun to show the devastating effect of resistance in cotton in America and deciduous fruit trees in Canada, US and Europe ((Kogan, 1998) and therein). The term integrated management has a long history of names before it became what is known today. It started off as pest control and later was changed into integrated control in late 1950s and the early 1960s because of the subsequent event of resistance development. The idea was already mentioned by Hoskins et al. (1939) and later defined by Stark (1971) as “applied pest control which combines and integrates biological and chemical control” (Kogan, 1998). Then in the mid-1970s pest management became synonymous to integrated control. However, Stark (1971) argued that pest control and integrated control should be considered differently. In 1972 the term integrated pest management (IPM), as it is known today, was accepted by the scientific community and incorporated in the scientific literature as “a decision support system for the selection and use of pest control tactics, singly or harmoniously coordinated into a management strategy, based on cost/benefit analyses that take into account the interests of and impacts on producers, society, and the environment” (Kogan, 1998).

This definition highlights the concurrent use of different pest control techniques such as biological control, habitat manipulation, modification of cultural practices, use of resistant varieties as well as the use of the right type and amount of pesticide to reduce human health risks and environmental pollution.

The cost-benefit analysis will determine the use of different tactics therefore the use of monitoring is in an integral part of IPM (Cloyd, 2009). Common methods to monitor pests are the use of traps or scouting collecting samples in the field/crops, which are later examined (Cloyd, 2009; De Veld et al., Voorjaar 2008)(Cloyd, 2009; De Veld et al., Voorjaar 2008). Then

economic threshold will be evaluated which is a concept that shows the different levels of IPM that compromise different tactical combination (Kogan, 1998). The aim is to use the lowest level where few interventions are applied whereby pest is controlled. Measurements on the use of pesticide have been the major factor if IPM successful (Weiss *et al.*, 2009) however more measurements are needed. The principle in using chemical controls is that the amount of synthetic ones are reduced and only used when utmost necessary and new biopesticides should be of better use.

3.2. Chemical control

It is evident from many literature studies ((Morse and Hoddle, 2006; Cloyd, 2009; Gao *et al.*, 2012) and online advice from agriculturists that chemical control of *Frankliniella occidentalis* is difficult, based on the problems described earlier. In crop protection insecticides are divided in two types: synthetic compounds and natural compounds. The latter consists of plant extracts. Synthetic compounds are also divided in either affecting a selective or broad spectrum of insect pests. An overview in *Table 1* gives commercially available chemical compounds to control *F. occidentalis*.

Table 1 Overview of synthetic and natural compounds used against thrips (*Thrips tabaci* and *Frankliniella occidentalis*). Adapted from Messelink & Kogel, 2012 and modification by adding the mode of action (with class noted in numbers) taken from the Insecticide Resistance Action Committee (IRAC) website <http://www.irc-online.org/pests/frankliniella-occidentalis/>

Type of compound	Trade name	Mode of Action
Natural of origin		
Pyrethrins & piperonylbutoxide	Spruzit	Alter sodium channel gating mechanisms (3A)
Azadirachtin	NeemAzal	Ecdysone antagonist (18B)
Selective chemical compounds		
Pyridalyl	Nocturn	Unknown
Lufenuron	Match	Chitin synthesis inhibitors (15)
Broad chemical compounds		
Spinosad (Spinosyns)	Conserve	Nicotinic acetylcholine receptor agonist and GABA chloride channel activator (5)
Abamectin (Avermectins, Milbemycins)	Vertimec	GABA chloride channel activator (6)
Thiamethoxam (Neonicotinoid)	Actara	Nicotinic acetylcholine receptor agonist (4A)
Methiocarb (Carbamate)	Mesurool	Acetylcholine esterase inhibitor (1A)
Esfenvaleraat (Pyrethroid)	Sumicidin	Alter sodium channel gating mechanisms (3A)
Deltamethrin (Pyrethroid)	Decis	Alter sodium channel gating mechanisms (3A)

Pyrethrins are the most widely used botanical insecticide (Ryan *et al.*, Retrieved March 2014). They are extracted from pyrethrum flowers (*Tanacetum cinerariifolium*), where they are predominantly found in the ovaries of the flower heads (Yang *et al.*, 2012a). They work as neurotoxins that bind to voltage-gated sodium channels of neuronal cells, causing the channels to remain open (Davies *et al.*, 2008). Pyrethrins compromise six closely related ester groups namely pyrethrin I and II, cinerin I and II, and jasmolin I and II (Ryan *et al.*, Retrieved

March 2014). Pyrethrins have been indicated to be responsible for the mortality and toxicity to adult and embryo of *F. occidentalis* therefore suggested to effect on feeding and oviposition both in vitro and in planta (Yang *et al.*, 2012a). Piperonylbutoxide (PBO) a microsomal monooxygenase inhibitor is mostly studied for its synergistic effect with other insecticides (Bielza *et al.*, 2008; Espinosa *et al.*, 2005; Jensen, 2000a) (Bielza *et al.*, 2008; Espinosa *et al.*, 2005; Jensen, 2000a; Jensen, 2000b). Azadirachtin is a commercially available pesticide originated from the neem tree and is also shown to be effective against *F. occidentalis* (Cloyd, 2009; Thoeming *et al.*, 2006). From the natural pyrethrins synthetic pyrethroids were also produced as can be seen in the table. However, *F. occidentalis* pyrethroids had developed resistance for them as well (Thalavaisundaram *et al.*, 2008). Since chemical control has short time effects they can be combined with other control techniques such as biological control. A list of insecticides that specifically combat *F. occidentalis* in the US can be read in the review of Cloyd, 2009. Selective compounds to control WFT in the US and in the Netherlands are pyridalyl and lufenuron, while spinosad, abamectin and methiocarb are compounds with a broad pest control spectrum including thrips. In addition, methiocarb and spinosad seemed to be mostly used worldwide. Even though spinosad was one of the most effective insecticides as reported by Shan *et al.* (2012) resistance to spinosad of adults has been reported in Australia (Herron and James, 2005) and south-eastern Spain (Bielza *et al.*, 2007b). Another insecticide used in Denmark and Australia is fipronil also a broad spectrum insecticide against *F. occidentalis* (Herron and James, 2005; Jensen, 2000b). In China a major study showed that from the 36 insecticides evaluated, phoxim is the most effective against the thrips. However, phoxim an organophosphate has a short life because it is rapidly degraded by UV light (Shan *et al.*, 2012). In addition, measures to delay resistance such as alternating or rotating insecticides from different mode of action groups have been researched (Bielza, 2008).

3.3. Biological control

Biological control makes use of natural predators, parasitoids or pathogenic microbes to reduce the population density of the pest. It is a “natural control” considering that some human interventions are still required to take care of the organisms applied. Predators are organisms that feed on one or more prey species to support their development and/or reproduction. Parasitoids oviposit and develop in or on a single host leading to death of the host (Din and Donchev, 2013). Pathogens are micro-organisms that cause disease in a host. Mites and bugs are among the different predators preying on thrips. Parasitoids such as wasps and pathogens such as nematodes and fungi infect thrips. In *Table 2* the most commonly used biocontrol agents, mostly commercially available are presented.

Table 2 Biological control agents of *Frankliniella occidentalis*. Adapted from Messelink & Kogel, 2012 and EPPO bulletin 2002 list of biological control agents.

Classification	Type of agent	First use	Commercially available
Predators			
Mites (foliar)	<i>Amblyseius cucumeris</i>	1985	World wide
	<i>Amblyseius barkeri</i>	1981	World wide
	<i>Amblyseius degenerans</i>	1993	World wide
	<i>Amblyseius californicus</i>	1985	Europe
	<i>Amblyseius swirskii</i>	2005	Europe
	<i>Amblyseius andersoni</i>	2007	Dutch market
	<i>Amblyseius montdorensis</i>	Past 3 to 4 years	Dutch market
	<i>Amblydromalus limonicus</i>	Past 3 to 4 years	Dutch market
Mites (soil-dwelling)	<i>Macrocheles robustulus</i>	2008	Europe
	<i>Hypoaspis aculeifer</i>	1995	Europe
	<i>Hypoaspis miles</i>	1994	Europe
Minute bugs	<i>Orius insidiosus</i>	1990s	North America
	<i>Orius laevigatus</i>	1990s	World wide
	<i>Orius albidipennis</i>	1991	Europe
Rove beetle	<i>Atheta coriaria</i>	2002	Canada
Parasitoids			
Parasitic wasp	<i>Ceranisus menes</i>	1996	Dutch market
Parasitic wasp	<i>Ceranisus americensis</i>	1996	Dutch market
Pathogens			
Entomopathogenic nematodes	<i>Steinernema feltiae</i>	2005	World wide
Entomopathogenic fungi	<i>Lecanicillium lecanii</i>	2012	Europe
	<i>Metarhizium anisopliae</i>	2012	Dutch market
	<i>Beauveria bassiana</i>	2012	Europe and America
	<i>Isaria fumosorosea</i>	2012	Dutch market

Predators

The predatory mite *Amblyseius (Neoseiulus) cucumeris*, introduced in 1980, was the first commercially used biological control agent against *F. occidentalis* in sweet pepper ((Messelink *et al.*, 2005) and therein). However, it was shown by Brodsgaard and Hansen (1992) that without presence of *F. occidentalis* the mite *N. cucumeris* did not survive. In addition, it was only effective in controlling *F. occidentalis* under high densities ((Messelink *et al.*, 2005) and therein). Therefore, other mite species were tested as biological control agents. *Amblyseius (Typhlodromalus) limonicus* (Gillespie P., 2010; Houten *et al.*, 1995), *Amblyseius (Typhlodromips) swirskii* and *Euseius ovalis* were observed to be more effective compared to *N. cucumeris* in cucumber (Messelink *et al.*, 2005) and *A. andersoni* in pepper (Van Houten *et al.*, 2005). *Euseius ovalis* is not commercially available yet (Messelink *et al.*, 2006). *Amblyseius degenerans* has been shown to suppress infestations of *F. occidentalis* on cucumber and pepper (Houten *et al.*, 1995; Messelink *et al.*, 2006; Van Houten *et al.*, 2005). For *Amblyseius (Neoseiulus) californicus* it was reported to be effective against *F. occidentalis* in pepper and in hot climates such as in Israel (Weintraub and Palevsky, 2008). *Amblyseius swirskii*, introduced in 2005, is now used worldwide for thrips as well as white fly control in some vegetable crops as well as chrysanthemum ((Messelink and Kogel, 2013; Messelink *et al.*, 2005) and therein). *A. swirskii* was more effective compared to *A. cucumeris* since the females were more aggressive towards thrips larvae. Furthermore, *A. cucumeris* was able to survive when food is scarce and able to cope with hot and dry climate greenhouse climates (Van Houten *et al.*, 2005; Wimmer *et al.*, 2008). Recently, in the past 3 to 4 years, *Amblyseius montdorensis* and *A. limonicus* are

increasingly used for biological thrips control in some vegetable crops as well as chrysanthemum (Messelink and Kogel, 2013) and therein).

Orius species (minute pirate bugs) are also used to biologically control *F. occidentalis* in pepper (Bosco *et al.*, 2008), starting in the 1990s. *O. insidiosus* was first used in North America and later on more species were tested (Messelink and Kogel, 2013). A field experiment in peppers showed that *O. insidiosus* could suppress both adults and larvae of *F. occidentalis* to almost extinction (Funderburk *et al.*, 2000). In contrast, *O. laevigatus* has gained worldwide importance in biological thrips control because it is easier to rear and develops quite quickly. However, during fall and winter both *O. insidiosus* and *O. laevigatus* control *F. occidentalis* inadequately because they enter diapause due to the short day length and thrips population would increase again (Tommasini *et al.*, 2002). *O. albidipennis* does not to enter diapause, and is thus used for biological control of WFT during fall and winter (Blaeser *et al.*, 2004).

Soil-dwelling predators

The soil-dwelling predatory mites *M. robustulus* (Messelink and van Holstein-Saj, 2008a), *Hypoaspis (Gaeolaelaps) aculeifer*, *Hypoaspis miles (Stratiolaelaps scimitus)* and the rove beetle *Atheta coriaria* are used as commercially available biological control agents against thrips in Europe. These, however, only target the soil stages, i.e. the pupae of *F. occidentalis*. A great deal of *F. occidentalis* would also hide within flower buds and pupate therein (Buitenhuis and Shipp, 2008)_so this is not an all rounded control. In addition, at high relative humidity most thrips pupate within the plant and not in the soil (Steiner *et al.*, 2011).

Parasitoids

Ceraninus menes and *C. americensis* are two parasitoid wasps shown to suppress WFT in chrysanthemum (Loomans, 2006). However, developing time is slow and failed in effectively controlling WFT ((Arthurs and Heinz, 2006) and therein).

Entomopathogens

Entomopathogenic nematodes (EPN) are another type of biological control that only target soil-dwelling stages of *F. occidentalis*. The commonly used nematode *Steinernema feltiae* is marketed in the UK and North America against *F. occidentalis* and leaf miners that infect ornamental and bedding plants (Arthurs and Heinz, 2006). Other EPN strains were also evaluated such as *Heterorhabditis bacteriophora* and *Steinernema carpocapsae* which are primarily used for combating but were less effective compared to *S. feltiae* due to its ability to infect both on mobile and non-mobile larvae of *F. occidentalis* (Ebssa *et al.*, 2001). It was shown, however, that early and regularly repeated application of these two species can control *F. occidentalis* (Belay *et al.*, 2005). *Thripinema nicklewoodi* is specialised in infecting parasite thrips during their feeding stages within the flower buds and foliar terminals. It is not commercialised because it is difficult to culture in mass production and only showed effectiveness in small scale (Arthurs and Heinz, 2006). The uses of EPN show potential in controlling WFT but only when applied at high concentrations and at favourable conditions. In addition, studies like the one from Arthur & Heinz (2006a) show variation in effectiveness and only for a few species.

Entopathogenic fungi (EPF) are also applied to control *F. occidentalis*. They can infect all life stages of *F. occidentalis* but their effects on the different stages differ (Ugine *et al.*, 2005). It seemed that adult thrips were more susceptible than immature ones (Messelink and Kogel, 2013). One possible explanation may be that as larvae pupate they shed their skin and lose the infection. The EPFs that control WFT the Netherlands can be seen in *Table 2*. One of them is *Metarhizium anisopliae* (Metschnikoff) which not only regulates *F. occidentalis* but also another pest *Otiorhynchus sulcatus* (black vine weevil) (Ansari *et al.*, 2008). The fungus, *Beauveria bassiana* has been proved to effectively control *F. occidentalis* in agricultural crops (Mukawa *et al.*, 2011). Even though *B. Bassiana* is a broad range pathogen of insects it did not show negative effect with *A. cucumeris* and has the potential to be combined when *A. cucumeris* cannot control WFT on its own (Jacobson *et al.*, 2001). A study on evaluating EPF showed that *Isaria fumosorosea* was able to cause higher mortality in WFT than the insecticide fipronil (Ansari *et al.*, 2008). For *Lecanicillium lecanii* it was found to affect all stadiums of *F. occidentalis* and the highest was observed for the adults (Vestergaard *et al.*, 1995). These last two were only studied in a laboratory setting and are commercially available to control other thrips (Ansari *et al.*, 2008). Similar to EPNs EPFs require a certain degree of humidity and the right time of application to get enough infection (Shipp *et al.*, 2003a) although EPNS can still be effective under low humidity (Mukawa *et al.*, 2011).

Combinatorial use of biological control agents

A combination of foliar and soil-dwelling predators would be an ideal biological control strategy. This is because soil-dwelling stages of the pest depend on relative humidity (Steiner *et al.*, 2011) when this is high they drop to the soil. In addition, host plant species also affect the dropping behaviour because in a close-leaf crop like lettuce they would not drop off to the soil (Steiner *et al.*, 2011). To increase efficacy of biological control different predators may be combined to achieve synergistic effects. As such as *O. insidiosus* and *A. degenerans* were combined on cut roses but the control levels were similar to those of using only *O. insidiosus* (Chow *et al.*, 2008). Although it was found that *O. insidiosus* not only preyed on *F. occidentalis* but also *A. degenerans* making *O. insidiosus* an intraguild predator. Another is the study on a combination of a predatory bug and mite in Dutch ornamental sector showing that both were successful in controlling thrips (Beerling and van der Linden, Retrieved March 2014). Research on interactions between two predatory mites' *A. swirskii* and *E. ovalis* against *F. occidentalis* and the greenhouse whitefly *Trialeurodes vaporariorum* showed that *A. swirskii* reduced the amount of thrips stronger than *E. Ovalis*. However, the control of the white fly was better by both predators when thrips were present than when they weren't. A mixed diet of *A. swirskii* indicated a positive effect on its predation behaviour (Messelink *et al.*, 2008b).

3.4. Cultural control

Pests have always been present within a population of plant species being influenced by intrinsic and extrinsic factors. Biological drivers such as life stages, reproduction and generation time controls *F. occidentalis* population density and dynamics (Morse and Hoddle, 2006; Nothnagl *et al.*, 2007). These intrinsic factors differ between pest species even within species (Nothnagl *et al.*, 2007). Extrinsic factors, including environmental cues such as temperature (Nothnagl *et al.*, 2008; Rhainds *et al.*, 2007), humidity (Steiner *et al.*, 2011) and

photoperiod (Whittaker and Kirk, 2004), food type such as plant pollen (Hulshof *et al.*, 2003), leaves (Brown *et al.*, 2002), flowers (Baez *et al.*, 2011; Kiers *et al.*, 2000), fruits (Baez *et al.*, 2011; Kiers *et al.*, 2000) and interactions with predators (Baez *et al.*, 2011; Kiers *et al.*, 2000) or other pests (Martini *et al.*, 2013; Messelink and van Holstein-Saj, 2008a) also affect the dynamics of the *F. occidentalis* population and thus their abundance. Ecological studies on the drivers of thrips population development may help to prevent *F. occidentalis* proliferation under glasshouse conditions to. However, for field conditions this is difficult to implement. Nevertheless, preventive measures to avoid favourable conditions for thrips development may be taken.

Cultural practices such as the application of fertilizers have shown to have a major effect on *F. occidentalis* growing on chrysanthemum (Chau and Heinz, 2006; Davies *et al.*, 2005), other ornamentals (Chow *et al.*, 2012) and agricultural crops (Brodbeck *et al.*, 2001; Reitz, 2002). Chau *et al.* (2005) reported that increasing fertilization reduced production time, the time necessary for chrysanthemums to bloom, and increased *F. occidentalis* population. However, the amount of insecticide application did not increase and the pest could be managed. Consequent research proved that by manipulating fertilization such as lowering it, it can be useful in controlling thrips. The results showed that lowering fertilization to 50% of the suggested level reduced *F. occidentalis* abundance to a mean of 44% and reduced fertilizer input for the production significantly (Chau and Heinz, 2006). In Davies *et al.* (2005) it was also noted that increased fertilizer affected chrysanthemum susceptibility to WFT meaning that higher fertilizer correlated with more feeding damage by the pest and that principally it was due to increased nitrogen in the plant. Another ornamental namely roses were evaluated on the response of *F. occidentalis* to different fertilization levels. The results showed that lowering the fertilization rate from 100% to 33% of the recommended level reduced *F. occidentalis* abundance by a mean of 30% (Chow *et al.*, 2012). It was also found in a study of tomato plants that increasing nitrogen fertilization resulted in higher populations of *F. occidentalis* in the plants (Brodbeck *et al.*, 2001). In addition, nitrogen and amino-acid content in flowers were measured and showed amino acids phenylalanine was correlated with female *F. occidentalis* abundance. Contrary to these Reitz (2002) observed no effect of different fertilization level on the populations of any of the thrips species which included *F. occidentalis*. However, they did not measure nitrogen content in the plants as they themselves pointed out. The fact that fertilisation had an effect proves that it may be a useful tactic in IPM by optimization of fertilizer level to reduce pest population growth (Chau and Heinz, 2006).

Mechanical control

Classical or common methods are practical matters like hygiene and weeding to prevent invading or contamination by pests. Trap plants are used to attract thrips in feeding on a more attractive plant than the crop being grown. Trap plants can then be removed or chemically treated, while the rest of the crop can be controlled with natural enemies, entomopathogenic fungi or nematodes (Buitenhuis *et al.*, 2007). An example is the use of attractive chrysanthemum cultivar to "pull" *F. occidentalis* away from the crop and to use a deterrent such as rosemary leaves to "push" the pest away (Bennison *et al.*, 2002). However, trap plants are more effective in stopping dispersing *F. occidentalis* to get to the crop plants and less effective against *F. occidentalis* that do not move away from the crop plants (Buitenhuis and

Shipp, 2006). Therefore a simultaneous use with a biological control like the predator *Orius laevigatus* would increase the efficiency of this tactic (Bennison *et al.*, 2002). In a field crop one strategy that is currently in use is the 'bare-earth' strategy which is a wide-scale removal of vegetation around the crops and glasshouse. However, this has some disadvantages such as being costly, loss of nutrients from the top-soil and high volumes of dust covering glasshouses, possibly blocking sunlight (Schellhorn *et al.*, 2010). Leaving native vegetation reduces these disadvantages, though it was studied in Australia where *F. occidentalis* isn't a native species on wild plants and remained in the crop plants. This strategy can be used only if surrounding vegetation has a positive effect on horticulture crops and if they are non-host and therefore not preferred by *F. occidentalis*. A different method is the use of ultraviolet-reflective mulch, in the form of raised-beds of plastic mulch. This prevents migration of adults *F. occidentalis* into crop plants (Funderburk *et al.*, 2011) because the UV radiation obscures the host location. Thrips locate suitable host plants partly through visual cues in the UV spectrum ((Reitz *et al.*, 2003) and therein).

Semiochemicals

One of the focuses in applied pest control is the study of adult insect behaviour causing it to leave the plant in search for better substrates (Outchkourov *et al.*, 2004a). Substances that can be used to influence insect behaviour are semiochemicals such as pheromones and kairomones. Pheromones can be divided in sex pheromones which are volatiles that attract the opposite sex, aggregation pheromones which attract both sexes and alarm pheromones which are released when insects are attacked and this causes avoidance or dispersal in conspecifics (Cook *et al.*, 2006). Kairomones are chemicals produced and emitted by the organisms to mediate interspecific interactions which benefit the receiver but not the emitter (Cook *et al.*, 2006). Moreover, volatiles or some type of compound such as oils released by plants to deter or attract insects also fall under the term semiochemicals. These chemicals are mostly used for a push and pull strategy where one odour compound attracts pests to the trap plants and the other repels them from crop plants (Bennison *et al.*, 2002; Cook *et al.*, 2006).

Odours that attract are used to pull pests out of their refuge which can either be sex pheromones (Teerling *et al.*, 1993), aggregation pheromones (De Kogel and Van Deventer, 2003; Hamilton *et al.*, 2005), host plant or food scents. Alarm pheromone decyl and dodecyl acetate was shown to reduce oviposition (Teerling *et al.*, 1993), induce larvae to fall from plants, increase take-off and decrease landing rates in adults *F. occidentalis* (MacDonald *et al.*, 2002). From the two male-produced compounds that have been identified (Hamilton *et al.*, 2005), one is commercially available as a lure for *F. occidentalis* population monitoring, having the trade name Thripline_{ams} (Syngenta Bionline, Essex, UK). It contains a pheromone which was first identified as a sex pheromone and changed to an aggregation pheromone because it attracts both males and females *F. occidentalis* (Hamilton *et al.*, 2005). The aggregation pheromone has also been added to blue sticky traps which showed an increasing capture of *F. occidentalis* up to 3× compared to traps without the pheromone ((Davidson *et al.*, 2007) and therein). Thripline and Thripher (Hamilton *et al.*, 2005) or Lurem-TR are semiochemicals commercially used for monitoring by attracting *F. occidentalis* (Davidson *et al.*, 2007; De Kogel and Van Deventer, 2003; Koschier *et al.*, 2000) and for mass trapping purposes (Hamilton *et al.*, 2005; Sampson and Kirk, 2013). Recently, in the order Thysanoptera, the first male produced

contact pheromone 7-methyltricosane has been identified (Olaniran *et al.*, 2013). This cuticular hydrocarbon of the adult male *F. occidentalis* attracted both male and female *F. occidentalis* in close contact compared to the aggregation pheromone neryl (S)-2-methylbutanoate which attracts male and female *F. occidentalis* over a distance (Hamilton *et al.*, 2005). On the other hand, repellents, such as alarm pheromones are used to prevent pest establishment. Alarm pheromones consisting of decyl acetate and dodecyl acetate have been identified for *F. occidentalis* (Teerling *et al.*, 1993) and were shown to disrupt feeding patterns and mating practices (MacDonald *et al.*, 2002). As *F. occidentalis* is a polyphagous species feeding on flowers they are attracted by common flower odours of these chemical class. Koschier *et al.*, (2000) evaluated the repellence or attractiveness of *F. occidentalis* to plant volatiles with a Y-tube olfactometer. It was observed that *F. occidentalis* was mainly attracted to flower odours that were common such as compound belonging to benzenoids and monoterpenes class (Kirk, 1985b). The benzenoids d anisaldehyde and the nicotinate ethyl nicotinate elicited attraction to *F. occidentalis* over a wide range of concentrations (Koschier *et al.*, 2000). The sesquiterpene eugenol and the benzenoids benzaldehyde only attracted at *F. occidentalis* at specific concentration (Koschier *et al.*, 2000).

Combinatorial use

Mechanical and biological control have also been applied together with semiochemicals. One combinatorial tactic is to lure by attraction and to kill by predators or pathogenic infection. An example for the combination of mechanical control and semiochemicals are the use of sticky traps with pyridine compounds. Ethyl and methyl isonicotinate are pyridine compounds that efficiently increased trap plant capture of adult *F. occidentalis* (Davidson *et al.*, 2007). Combining biological control with semiochemicals the fungus *Metarhizium anisopliae* was used in a trap device together with Lurem-TR containing methyl-isonicotinate as the active compound to combat *F. occidentalis* in French bean (Niassy *et al.*, 2012). Combination of the fungus and the semiochemical increased attraction of thrips to the trap but the attractant negatively affected the persistence of fungal conidia (Niassy *et al.*, 2012). A way to solve this is to screen for semiochemicals that are compatible with the insect pathogen (Niassy *et al.*, 2012). Dodecyl acetate component of the alarm pheromone mixed with the insecticides maldison showed significant reduction in larvae numbers of *F. occidentalis* (Cook *et al.*, 2002).

Host plant resistance

In nature, plants have always defended themselves against multiple stress factors which are biotic and abiotic of origin (Pieterse *et al.*, 2009). Examples of abiotic factors are wind, temperature, nutrient, water, oxygen and soil pH changes (Scheffer, 1996). Biotic factors are pathogens such as fungi, viruses and bacteria, parasitic organisms and herbivorous insects (Pieterse *et al.*, 2009). To withstand these multiple stress factors, plants have developed a complex immune system consisting of constitutive and inducible defences. Constitutive defences are trichomes, spines, cuticula and constitutively produced antimicrobial metabolites. Trichomes and spines are morphological features that prevent herbivores from eating the plant (Traw *et al.*, 2003). Preformed antimicrobial compounds are produced during plant development and are stored in trichomes, oil glands and epidermal cells. Glandular trichomes in particular have been extensively reported as effective defences against many different pests

(Simmons and Gurr, 2005). Moreover, primary (Mollema and Cole, 1996) and secondary (De Jager *et al.*, 1996; Leiss *et al.*, 2009a; Tsao *et al.*, 2003) compounds produced by the plant have shown to affect thrips feeding behaviour and thus its biology. For the inducible defence depending on the type of attack, plants will synthesize one or more phytohormones that signal the activation certain defence. Salicylic acid (SA) is produced against biotrophic pathogens, jasmonic acid (JA) against necrotrophic pathogens and insect herbivory and Ethylene (ET) which can act synergistically with JA (Pieterse *et al.*, 2009; Yang *et al.*, 2011). Many studies on defence signalling have shown that several responsive genes are always activated upon a certain attack and are called marker genes. The well-characterized marker genes are PATHOGENESIS-RELATED₁ (*PR-1*) for SA response, VEGETATIVE STORAGE PROTEIN₂ (*VSP₂*) for JA response and PLANT DEFENSIN_{1.2} (*PDF_{1.2}*) for JA and ET response. Apart from phytohormones other compounds are produced after induction such as digestive inhibitors (e.g. Protease Inhibitors PIs), enzymes (e.g. polyphenol oxidases) and a range of secondary metabolites (e.g. nicotine). Host plant resistance studies have therefore been aiming to identify cultivars that are resistant to *F. occidentalis* on feeding or oviposition measurements ((Fery and Schalk, 1991; Harrewijn *et al.*, 1996; Tsao *et al.*, 2003) or to plant viruses transmitted by thrips (Funderburk *et al.*, 2011). There are three types of mechanisms described that confer host plant resistance due to measurements of the pests' biology. Host plant resistance is either by tolerance, antixenosis or antibiosis. Plant tolerance was defined as: "All plant responses resulting in the ability to withstand infestation and to support insect populations that would severely damage susceptible plants" – Horber, 1980 (Fery and Schalk, 1991)

Antixenosis affect the pest behaviour whereby there is a reduced preference of the pest leading to lower oviposition and/or feeding. On the other hand antibiosis affects the physiology of the pest thereby reducing its survival and/or reproduction (Fery and Schalk, 1991; Maharajaya *et al.*, 2012).

Morphology

Host plant resistance due to morphological trait against *F. occidentalis* is sparse in the literature. One example is the study by Felland *et al.* (1995) on the distribution of thrips in nectarine orchards where they observed that *Frankliniella occidentalis* preferred nectarine than peaches of the same hosts' species due to nectarines having smoother tissue (Northfield, 2005). In addition, Northfield (2005) described other examples such as leaf surface wax, epidermal cell wall thickness and pollen stickiness are traits that contribute to host plant defence against thrips, however, these were not found for *F. occidentalis* (Northfield, 2005). Moreover, studies on carrot silver damage did not correlate with morphological traits such as plant size, leaf hairs or leaf area. This report was also consistent with previous studies on morphological traits and thrips resistance in chrysanthemum (De Jager *et al.*, 1996), Senecio (Leiss *et al.*, 2009b) or tomato (Mirnezhad *et al.*, 2010).

Chemical

Fertilizers that affect the host plant also affect insect preference and biology therefore study on host plant resistance has been available since the 1990s (De Jager *et al.*, 1993; Fery and Schalk, 1991). However, it is only recently that the underlying mechanisms are known (De Jager *et al.*, 1996; Leiss *et al.*, 2009a; Tsao *et al.*, 2003)(De Jager *et al.*, 1993). For *F. occidentalis* the oldest

study on resistant cultivars originates from the 1990s. In 1991 Fery & Schalk investigated pepper germplasm for the resistant cultivars to WFT. Damage on leaves due to feeding, larval and adult insect density, plant height, and shoot fresh weight were measured. They observed that peppers were resistant to *F. occidentalis* based on tolerance mechanisms (Fery and Schalk, 1991). For cucumber cultivars it was discovered that resistance to *F. occidentalis* was based on effects on reproductive fitness and not adult mortality (Soria and Mollema, 1995). This variation is the antixenosis host plant resistance mechanism because reproduction rather than adult survival was affected. In cucumber varieties WFT damage was negatively correlated with low aromatic acid content (Mollema and Cole, 1996). The use of this nutritional compound is a good selection criterion in breeding resistance crops. In addition, the detrimental effect on *F. occidentalis* will make it easier to combine with biological control but further research is necessary since insect predators may also be affected by these primary metabolites. Therefore this resistance mechanism against *F. occidentalis* is based on antibiosis.

Secondary metabolites

As seen in many studies cucumber (Mollema and Cole, 1996), pepper (Fery and Schalk, 1991), chrysanthemum (De Jager *et al.*, 1995) host plant resistance to WFT occurs and that there was an indication that this was due to secondary metabolites (De Jager, 1995). A study on metabolite profiles of using high performance liquid chromatography (HPLC) to chrysanthemum cultivars with varying degrees of host-plant resistance against WFT led to the discovery of isobutylamide (Tsao *et al.*, 2003). Moreover, a metabolomic approach of comparing metabolomic profiles of *Senecio* hybrids but using a nuclear magnetic resonance spectroscopy (NMR) revealed two pyrrolizidine alkaloids and a flavanoid be related to thrips resistance (Leiss *et al.*, 2009a). The pyrrolizidine alkaloids were jaconine and jacobine, and kaempferol glycoside as the flavanoid. Further using this technique chlorogenic and feruloyl quinic acid were identified as resistance factors in chrysanthemum against WFT (Leiss *et al.*, 2009b). In tomatoes, another host plant of *F. occidentalis*, the same metabolic approach using NMR revealed that thrips resistant tomatoes had a different metabolic profile than susceptible tomatoes. In addition, acylsugars were identified as the thrips resistance factor in tomatoes (Mirnezhad *et al.*, 2009). The use of NMR had shown to be a good approach to identify candidate compounds involved in WFT resistance so an eco-metabolomic approach had been described and further researched in carrot cultivars (Leiss *et al.*, 2011).

Volatiles

Volatile compounds that are emitted due to insect damage are mainly reported to be monoterpenes and sesquiterpenes ((Yang *et al.*, 2013) and therein). Linalool is a monoterpene which occurs in a wide variety of flowering plants and has been suggested to play a role in direct and indirect plant defence against several herbivores ((Yang *et al.*, 2013) and therein).

Transgenic plants

The earliest study on protease inhibitors (PIs) was on the serpin elastase inhibitor expressed in transgenic alfalfa which delayed *F. occidentalis* damage. However, overall PIs were not characterized. Moreover, their effect on insect protease and adult oviposition rate were not looked at (Thomas *et al.*, 1994). A large part of the literature focuses on the PIs effect on larvae

which require protein for their growth and development. PIs were observed to delay larval development, stunt growth and increase larval mortality (Jongsma and Bolter, 1997). Identification of PIs that effect *F. occidentalis* showed that oviposition rates were affected by cysteine PIs (Annadana *et al.*, 2002). However, a following experiment, on expressing potato multicystatin in florets of chrysanthemum to evaluate the effect on WFT, conferred the opposite with no effect on the thrips ((Leiss *et al.*, 2009b) and therein). Further studies by Outchkourov *et al.*, (2004a) confirmed the effects of cysteine protease inhibitors on adult female *F. occidentalis* affecting population development. This effect was based on deterrence and reduction of fecundity ((Outchkourov *et al.*, 2004a) and therein). Engineering multidomain protease inhibitors into transgenic potato plants for resistance against thrips confirmed the ability of cysteine PIs to suppress the fecundity of *F. occidentalis* and reduce survival rates (Outchkourov *et al.*, 2004b). However, this has not been implemented in practice since PIs can affect not only the pest but other non-target organisms as well. Another study combined attraction of *F. occidentalis* and deterrence due to bad taste. A linalool synthase (LIS) was over expressed in transgenic chrysanthemum plants whereby monoterpene linalool/nerolidol synthase was produced in the aerial parts of the plant. The emissions of linalool attracted *F. occidentalis* for the first 15 min but due to accumulation of several forms of linalool glycosides *F. occidentalis* changed their preference from the transgenic to the control wild type plants (Yang *et al.*, 2013). This combinatorial tactic of attraction and deterrence by the flowers optimizes the seed yield for the plant due to attraction of pollinator and deterrence of pests as suggested by Yang *et al.*, (2013).

Induced resistance

Inductions of defence are the responses of plants to a variety of pests that are present which are not only insect herbivores but many pathogens that are either biotrophic or necrotrophic in lifestyle (Pieterse *et al.*, 2009). Each pest turns phytohormones signalling pathways on. These effect leads to the cross-communicating signalling pathways of salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) (De Vos *et al.*, 2005). In *Arabidopsis* plants exposed to *F. occidentalis* showed that JA biosynthesis genes were stimulated (De Vos *et al.*, 2005). The JA-responsive marker genes *VSP2* and *PDF1.2* were also induced and the majority of the changes in JA-responsive gene expression were specific to this attacker (De Vos *et al.*, 2005). This confirms that for the defence against cell-content-feeding herbivores JA plays a major role. Moreover, mutant plants compromised in JA showed enhanced susceptibility to thrips feeding and overexpression the signal peptide involved in the wound-induced expression leading to PIs production that caused reduced thrips damage (Li *et al.*, 2002). A wide variety of alkaloids are also known to have been identified such as pyrrolizidine alkaloids (PAs) (Macel *et al.*, 2005) that are related to resistance to this generalist insect pest (Van Doorn and De Vos, 2013). From the plant *Senecio vernalis* Senkirkine a PA was found to be most effective to thrips (Macel *et al.*, 2005). Food preferences are also affected by defence responses. Methyl jasmonate (MJ)-induced defence responses in plants provoked changes in food preferences of *F. occidentalis* preferring non-induced plants instead (Thaler *et al.*, 2002). However, the induction of plant defence is of advantage to TSWV because it seems to be activated by SA biosynthesis and SA-regulated plant defences which negatively affect wound-induced JA-regulated plant defence (Abe *et al.*, 2012). This decrease in JA-regulated genes caused thrips to prefer *Arabidopsis*

infected with TSWV plants. This was validated by thrips not preferring JA- insensitive *coi-1* mutant plants in contrast SA treated wild-type *Arabidopsis* (Abe *et al.*, 2012).

Combinatorial use

Many studies show that resistant cultivars exist in cucumber (Mollema and Cole, 1996), pepper (Fery and Schalk, 1991), chrysanthemum (De Jager *et al.*, 1995), however, a combination with biological control and the possible effects of host plant resistance to the tactic is not available. However, it is shown that biological control using the predatory mite, *Amblyseius cucumeris* and *Orius* spp. have been effective in controlling *F. occidentalis* on greenhouse sweet pepper and cucumber ((Shipp and Wang, 2003b) and therein). Moreover, not many studies are done on biological control on tomatoes because as suggested by Shipp & Wang (2003a) researchers speculate glandular trichomes on tomatoes would secrete sticky exudates all over the plant hindering the predator. However, they proved that this is not so because *A. cucumeris* was able to effectively control of *F. occidentalis* on greenhouse tomatoes but the release of *O. insidiosus* failed to do so (Shipp and Wang, 2003b).

Breeding of host plant resistance

Several studies on NMR as a tool in identifying metabolites involved in herbivore resistance proves to be potentially promising for breeding programs because it comprises a significant advance in the study of plant-insect relationships (Leiss *et al.*, 2011; Mirnezhad, 2011). In addition, wild cultivars are sources of genes for resistance to herbivores (Mirnezhad *et al.*, 2010). On the other hand cultivated crops have lost these genes through out breeding (Hull-Sanders and Eubanks, 2005). Breeding crops with wild relatives or resistant cultivars that are identified can improve crop production and quality (Fery and Schalk, 1991). Methods that could select for cultivars at a fast and easy way without time consuming practices such as screening would also improve production of resistant cultivars. An example is the use of molecular markers such as quantitative trait loci (QTLs) in mapping for resistance in beans against *T. palmi* (Frei *et al.*, 2005). With the large genomic sequencing of thrips this can be done to *Frankliniella occidentalis* and finding molecular markers in assisting in breeding selection. Another way is to screen for resistant individuals against *F. occidentalis* within a cultivar using the electronic nose (EN), which is an analytical instrument that mimics the human nose (McKellar *et al.*, 2005). The EN was used to detect volatiles, which are correlated with resistance, released from leaf disks and to later validate the level of resistance to *F. occidentalis*. However, EN is not able to identify the type of compound from the volatiles. More studies are needed for this technique.

4. Future outlook

The principle of **IPM** is to combine a whole array of tactics to diminish pest damage and at the same time reduce pesticide use and therefore the negative effect impacting humans and the environment. Monitoring/Scouting is an integral part of IPM it is one a methods in detecting, preventing and controlling *F. occidentalis* at an economic threshold. There are many different methods in controlling *F. occidentalis* but a combination of all tactics for the implementation for IPM are still lacking. The combination with **chemical control** can be hard because application of broad insecticides affect biological control; it kills natural enemies of thrips. In addition, selective insecticides are limited and do not reduce thrips population enough to prevent damage. Moreover, they are limited due to new regulations. The combination of **biological control** with cultural control has shown promise such as volatiles attracting pest in trap plants where predators can reside. In addition, it offers an economic, sustainable and safe alternative to chemical control. However, certain predator species are hard to produce in massive quantities and application techniques need to be improved for entopathogens (nematode and fungi). Moreover, natural predators have difficulty in establishing in ornamental crops. **Cultural control** is an essential part that has been and always will be needed for part of IPM mainly because it works. The combination with biological control even showed increased efficiency. However, a combination of host plant resistance with biological control and the possible affects are unknown and need further research. Moreover, resistant cultivars do not fully stop the spread of TSWV because a study on resistant pepper varieties showed that they had minor effect on the primary spread of TSWV (Maris *et al.*, 2003a). The preceding study did report that decreased oviposition rates and increased larval mortality on resistant varieties hindered WFT population development and secondary spread of TSWV (Maris *et al.*, 2004).

The molecular tools that are available, however, help to identify the mechanisms of resistance and facilitate breeding for resistant cultivars. Improvement in detecting the pest will help prevent or make the right use of tactics. The molecular tools in detecting these pests show potential. An example is the use of PCR-based sequencing in detecting *F. occidentalis* at an early phase when symptoms aren't apparent (Brunner *et al.*, 2002; Huang *et al.*, 2010). Another improvement is the use of entopathogenic nematodes which work but only at soil level and are also expensive. Making use of better application methods such as sprays with better coverage or solutions that will keep the nematodes at the location of treatment (Brusselman *et al.*, 2012) will improve the efficiency. However, these need to be already available for the farmers because investing in new materials is not something they will do if not approved to be super effective. Moreover, the costs will be cheaper if the materials are easily available or producible. A whole network of ecological niche of predators at many levels such as foliage, soil and air would be the perfect tactic. Therefore more studies on this would be necessary.

It would have been nice to consider the cost difference between chemical insecticides and natural compounds. In addition, chemical control versus biological control to see if a combination would fair cheaper than only biological control. It is known that use of entopathogenic nematodes are expensive since they are hard to rear, much less is entopathogenic fungi but other factors such high relative humidity causes other pathogens to infest such as oomycete or pathogenic fungi. Moreover, knowledge if farmers are fully aware of

the resistance development and that they do take good care with the use of chemical compounds is not known. Awareness and training for IPM implementation are necessary to understand the right use of the different tactics. Another gap in the knowledge is that many methods and discoveries are not known if they are indeed implemented. Most experimental trials are set in a laboratory which is a small scale study and would still be implemented in a large scale such as glasshouses which is a totally different settings possibly not conferring the same results as in the laboratory. Again not every company will admit to having this pest or be gladly to have this pest at their glasshouse making it hard to continue the research on a large scale. Moreover, in the laboratory an array of techniques are used to follow thrips behaviour (Harrewijn *et al.*, 1996; Wetering *et al.*, 1998) or host compound (Mirnezhad *et al.*, 2010; Yang *et al.*, 2013) which in a large scale may completely differ in ecological and biological aspects.

Understanding both the pest and host plant in a biological and ecologic way has led to the improvement in controlling of *F. occidentalis* not to mention the biotechnological advancements that helped with the progress. Moreover, investing in further research to tackle upcoming problems and to constantly educate is necessary. Studies on the interactions of multiple tactics are necessary to be evaluated if they match within IPM programme and can be implement in combating *F. occidentalis*.

In my opinion it is worthwhile in implementing IPM because of its broad scale of tactics which makes it complex but at the same time versatile to produce a sustainable and long term management of pest species. From my point of perspective biological control in combination with cultural control have shown great advancement in research as well as in implementation. The information is out there and there have been many studies and website that propagate this data but the question is, is it implemented everywhere?

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