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Incidence and molecular mechanisms of insecticide resistance in *Frankliniella occidentalis, Thrips tabaci* and other economically important thrips species

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With 3 figures and 5 tables

Abstract: Thrips species (Thysanoptera) damage plants by direct feeding and transmitting plant viruses and are considered one of the most harmful insect pests on crops worldwide. Their control mainly relies on the use of insecticides, but due to their frequent use and several biological aspects of thrips, insecticide resistance has arisen. However, despite its economic impact, the molecular mechanisms of thrips resistance have been poorly investigated. Resistance mutations in genes encoding the target-sites of insecticides have been infrequently reported for only five target-site genes. As an illustration of the lack of knowledge, analysis of publicly available sequencing data revealed the presence of acetylcholine esterase resistance mutations A201S and F290V, which had not yet been reported from the field. Next, we also summarize the importance of metabolic resistance, historically inferred mainly from data from enzyme activity assays and synergism studies. As these only suggest main routes of detoxification without providing details on underlying genetic mechanisms, the rapidly changing availability of genomic data provides an impetus to dissect causal genes. As not all main detoxification families were annotated in the main species, we took advantage of recently published thrips genomes to annotate and compare the glutathione-S-transferase (GST) family of *Frankliniella occidentalis* and found a relatively higher number of sigma GSTs. A broader understanding of the molecular mechanisms of resistance and especially the identification of resistance mutations and key detoxification enzyme genes will drive the development of molecular diagnostic tools that can be used for monitoring insecticide resistance in thrips.

Keywords: Thysanoptera, target-site insensitivity, metabolic resistance, detoxification enzymes, acetylcholine esterase, glutamate-gated chloride channel, resistance management

1 Introduction

The insect order of the Thysanoptera comprises about 5,000 thrips species including some of the most dangerous crop pests (Fig. 1; Mound & Teulon 1995). Thrips are one of the major pests in agriculture worldwide being responsible for high yield losses and economic damage (Diaz-Montano et al. 2011; Reitz et al. 2020). Via feeding and oviposition, they cause significant damage to plant tissues, which is particularly deleterious for ornamental cultures (Diaz-Montano et al. 2011; Gao et al. 2012). Thrips are also known to be a vector of several plant viruses of the genera Tospovirus, e.g., tomato spotted wilt virus (TSWV), affecting important crops and resulting in severe economic damage (Gupta et al. 2018; Jones 2005).

Although biological control has a significant role in thrips management in greenhouses (Nguyen et al. 2019; van Lenteren et al. 2018), their control mainly relies on the use of insecticides as easy to use and highly effective crop protection tools (Mouden et al. 2017). However, due to the withdrawal of some insecticides from the market and difficulties in the registration of new molecules, insecticide control strategies of thrips are in some regions, for example in the European Union, limited to only a few active compounds (Isman 2019; Van Leeuwen et al. 2020). In addition, thrips tend to develop insecticide resistance very rapidly, which has been attributed to some of their biological characteristics as well as to the high spray frequency required to control their populations. Thrips exhibit different forms of haplodiploid reproduction including arrhenotoky, which is characterized

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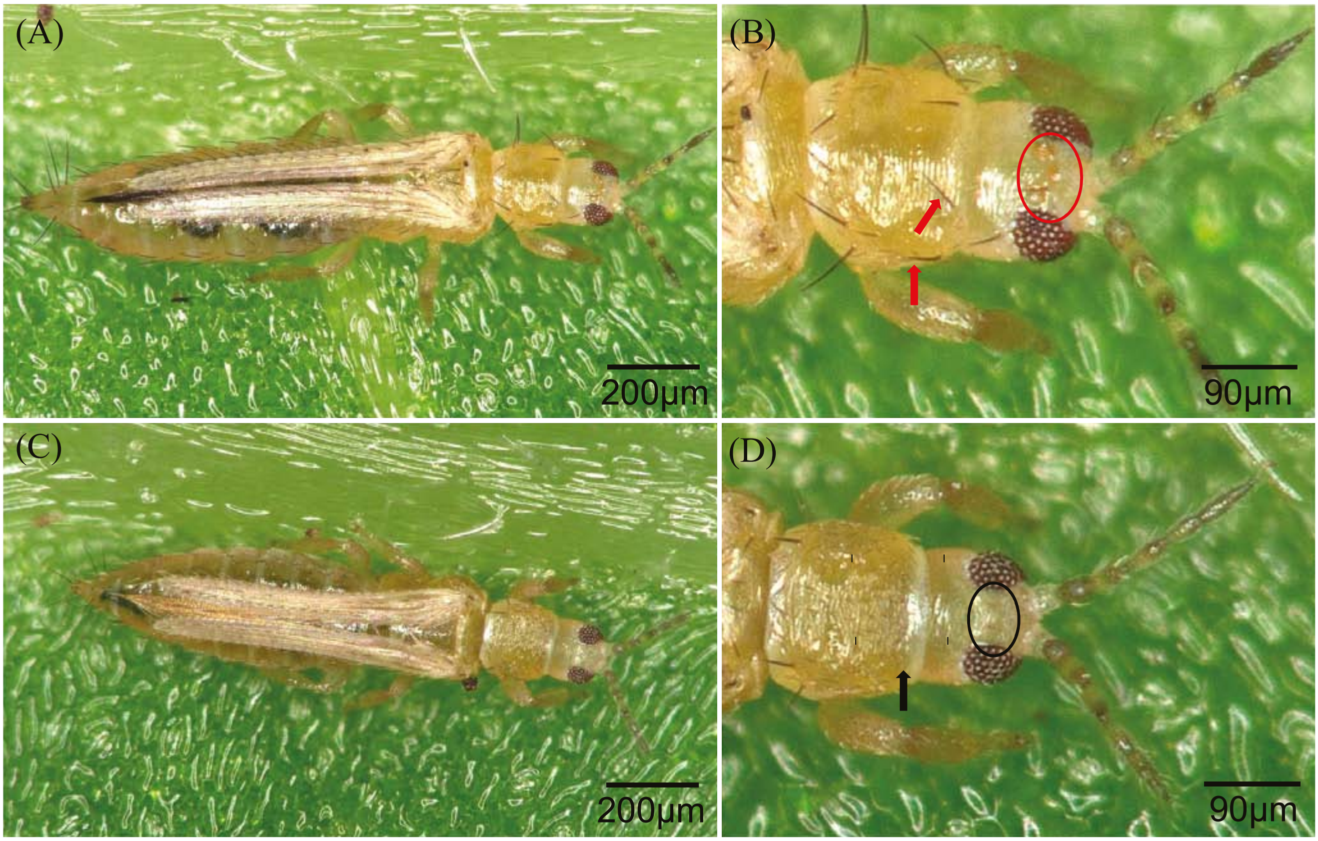

Fig. 1. Adult female of *F. occidentalis* **(A)**, detail of the *F. occidentalis* head-pronotum region **(B)**, adult female of *T. tabaci* **(C)**, detail of the *T. tabaci* head-pronotum region **(D)**. Red arrows indicate setae on the anterior part of the pronotum of *F. occidentalis* that can be used as taxonomic key to distinguish thrips species (Cluever & Smith 2017; Wang et al. 2019); black arrows indicate the same position on *T. tabaci* where the setae are not present. A red circle indicates the reddish colored ocelli of *F. occidentalis* while a black circle points towards the grey ocelli of *T. tabaci*, which are not clearly visible in the image. Thrips images were taken with a Keyence VHX-970F digital microscope equipped with Z20 lens at 200× magnification.

by production of haploid males that directly expose resistance alleles to selection (Gao et al. 2012), and thelytoky were diploid females arise from unfertilized eggs (Jacobson et al. 2013; Kumm & Moritz 2010; Nault et al. 2006). Thelytoky mechanisms in insects can be either induced by maternally inherited bacteria (e.g., Wolbachia), which usually result in complete homozygosity of the offspring due to gamete duplication, or caused by genetic factors, which may maintain the heterozygosity (Nguyen et al. 2015). Molecular mechanisms underlying thelytoky in thrips are not yet clarified. Earlier studies on the obligate thelytokous thrips *Heliothrips haemorrhoidalis* indicate meiotic parthenogenesis through terminal fusion as its reproductive strategy (Nguyen et al. 2015). More recently, antibiotic and heat treatments have suggested that bacterial endosymbionts are involved in *Franklinothrips vespiformis* reproduction (Arakaki et al. 2001), but not in *H. haemorrhoidalis* (Nguyen et al. 2015). However, since the type of parthenogenesis influence the genetic variability and levels of homozygosity of the offspring, and therefore the dynamics of insecticide resistance, further investigations on other economically important species (e.g., *T. tabaci*) would be particularly relevant. Further, many thrips species have a short generation time with overlapping generations and exhibit high fecundity (Ding et al. 2018; Nault et al. 2006; Reitz et al. 2020). Many of these properties are shared with the spider mite pest *Tetranychus urticae*, which also develops resistance extremely fast (Van Leeuwen & Dermauw 2016). Like spider mites, many thrips species are highly polyphagous insects and equipped with a wide array of detoxification enzymes (Dermauw et al. 2013b; Guo et al. 2020a; Rotenberg et al. 2020; Yue et al. 2022), which have been suggested to predispose the development of resistance (Dermauw et al. 2018; Rane et al. 2016). Resistance to most compounds used for thrips control has been reported for the most harmful species, including cosmopolitan invasive pests such as western flower thrips (*Frankliniella occidentalis*, Fig. 1), onion thrips (*Thrips tabaci*, Fig. 1), melon thrips (*Thrips palmi*) and flower thrips (*Frankliniella intonsa*; e.g., Diaz-Montano et al. 2011; Gao et al. 2012). However, molecular mechanisms underlying resistance (for an overview see below) have not been thoroughly investigated compared to other major pests. Enzymatic assays and synergism studies allowed to obtain some general information on the contribution of increased metabolism in resistance, without identifying specific genes. Similarly, the incidence of target-site resistance mutations has been only poorly studied and currently resistance-associated mutations in thrips have only been identified in five genes: (1) the voltage gated sodium channel (VGSC), (2) the nicotinic acetylcholine receptor (nAChR), (3) the chitin synthase 1 (CHS-1), (4) the glutamate-gated chloride channel (GluCl) and (5) γ-aminobutyric acid (GABA) receptor (Rdl). Understanding the molecular mechanisms is of crucial importance to allow the development of easy-to-use diagnostic tools to monitor resistance incidence in a high number of individuals and populations (Van Leeuwen et al. 2020). Although diagnostic tools are not yet readily implemented in agricultural settings, they might be soon implemented to maintain pesticide efficiency guiding the selection of effective pesticides and avoiding selection for resistance (R4P Network 2016). This review aims to overview and update, ten years after the last published overview (Gao et al. 2012), our understanding of the incidence and molecular mechanisms of insecticide resistance in thrips, and to identify possible gaps of knowledge that should provide an impetus for future studies.

2 Incidence of thrips resistance

Over the last decades, thrips species have developed resistance towards all the main insecticides used for their control. Table 1 provides a list of the currently most used products in thrips control in 2021 worldwide, sorted according to acreage use (data contributed by Dr. Ralf Nauen). Gao and colleagues reviewed insecticide resistance cases in *F. occidentalis* in 2012 (Gao et al. 2012) and, since then, the number of reported cases as well as the number of active ingredients to which thrips developed resistance, has increased dramatically. Table 2 and Figure 2 provides an overview of the number of reports per compound and species, while a case by case overview is presented in Table S1.

Resistance to carbamates and organophosphates, which act as acetylcholine esterase (AChE) inhibitors (respectively classes 1A and 1B of the Insecticide Resistance Action Committee (IRAC) mode of action (MoA) classification), and pyrethroids, modulators of the sodium channel (class 3A), was first reported decades ago, but continues to evolve worldwide, e.g. in the United States (Adesanya et al. 2020), Mexico (Cubillos-Salamanca et al. 2020), Israel (Lebedev et al. 2013), Ethiopia (Negash et al. 2021), Iran (Nazemi et al. 2016), Japan (Jouraku et al. 2019) and China (Wang et al. 2016). Neonicotinoids are nAChRs competitive modulators (class 4). Resistance to this class of insecticides is of increasing concern, and numerous resistant populations have been identified (Bao et al. 2015; Fu et al. 2019; Gao et al. 2014; Huseth et al. 2016; Minakuchi et al. 2013; Wang et al. 2016). Resistance cases to the class of spinosyns, comprising spinosad and spinetoram, have been steadily increasing in thrips (Cubillos-Salamanca et al. 2020; Fu et al. 2018, 2019; Gao et al. 2021; Sun et al. 2022; Wang et al. 2016; Zhang et al. 2022a). Spinosyns are allosteric modulators of nAChRs (class 5) and are widely used in thrips control

Table 1. An overview of the most utilized products in thrips control in 2021 worldwide, sorted according to acreage use. The number of reported resistance cases is indicated.

MoA	Active Ingredient	Since 2012	Total*
5	Spinosad	14	19
3A	Lambda-Cyhalothrin	3	6
3A	Acrinathrin	2	11
23	Spirotetramat	0	0
4A	Acetamiprid	2	0
3A	Deltamethrin	1	9
6	Abamectin	4	7
unknown	Azadirachtin	0	0
1A	Formetanate	0	7
3A	Fluvalinate	0	1
3A	Pyrethrins	0	0
3A	Esfenvalerate	0	1
3A	Cypermethrin	5	14
28	Cyantraniliprole	1	1
5	Spinetoram	8	8
28	Chlorantraniliprole	0	0
unknown	Pyridalyl	1	1
3A/4A	Deltamethrin+Thiacloprid	0	0

*Based on the resistance cases reported in Table S1

Table 2. The number of reported resistance cases in thrips, grouped according to insecticide mode of action.

MoA	Class	Since 2012	Total*
1A	Carbamates	3	20
1B	Organophosphate	8	19
2A	Cyclodiene organochlorines	0	2
2B	Phenylpyrazoles	0	1
3A	Pyrethroids	14	47
4A	Neonicotinoids	11	12
5	Spinosyns	22	27
6	Avermectins, Milbemycins	7	10
7C	Pyriproxyfen	1	1
15	Benzoylureas	1	1
28	Diamides	1	1
UN	Pyridalyl	1	1

*Based on the resistance cases reported in Table S1

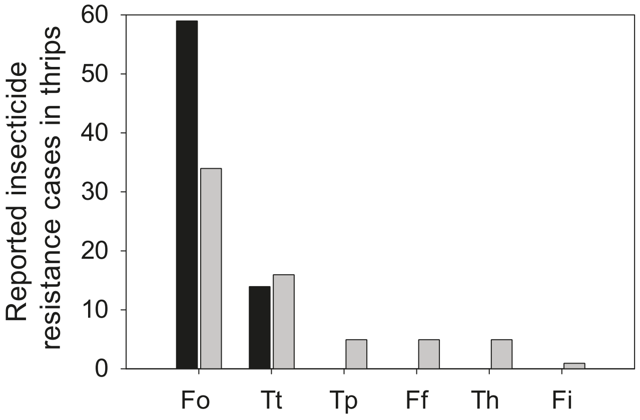

Fig. 2. Number of reported insecticide resistance cases in *F. occidentalis* (Fo), *T. tabaci* (Tt), *T. palmi* (Tp), *Frankliniella fusca* (Ff), *Thrips hawaiiensis* (Th) and *F. intonsa* (Fi). Black and gray histograms indicate insecticide resistance cases reported before 2012 and after 2012, respectively (details are provided in Table S1).

(Table 1) due to their high efficacy and the lack of reliable alternatives (Sparks et al. 2012). Hence, the increase of spinosyn resistance is of great concern for a reliable thrips management. Resistance to abamectin and emamectin benzoate, acting as allosteric modulators of the glutamate chloride channel (GluCl; class 6), has been reported in three thrips species (Adesanya et al. 2020; Chen et al. 2011; Gao et al. 2021; Herron et al. 2014; Meng et al. 2018). Finally, recent evidence of *F. occidentalis* resistance to the juvenile hormone mimic – pyriproxyfen – (class 7C; Wang et al. 2016), the inhibitor of chitin biosynthesis – novaluron – (Class 15; Suzuki et al. 2017), the compound of uncertain mode-of-action – pyridalyl – (Wang et al. 2020b), and the ryanodine receptor modulator – cyantraniliprole – (class 28; Wang et al. 2016) has also been documented. Despite the many reported resistance cases and the exceptional economic importance of thrips, only few studies tried to elucidate resistance mechanisms. In most cases investigation focused on biochemical and toxicological assays inferring general metabolic resistance, hereby overlooking target-site insensitivity by the lack of molecular tools and sequence data, inevitably providing an incomplete view of resistance mechanisms.

3 Molecular mechanisms of thrips resistance

The development of resistance is an evolutionary phenomenon and the mechanisms of insecticide resistance have been extensively reviewed (Feyereisen et al. 2015; Van Leeuwen & Dermauw 2016). Two mechanisms can be distinguished from a physiological and biochemical perspective. Toxicokinetic mechanisms include increased metabolism, reduced penetration, sequestration, increased excretion and increased efflux of the toxicant, which ultimately result in a decreased exposure to the pesticide. Increased metabolism is especially well studied, although the other mechanisms have been the subject of recent studies as well (Balabanidou et al. 2018; Heckel 2014; Kennedy & Tierney 2013). Toxicodynamic mechanisms comprise changes of the target-site of the pesticide, ultimately leading to a decreased sensitivity to the toxicant and have been identified as an important resistance mechanism in innumerable insect species (Feyereisen et al. 2015). These mechanisms are driven by three types of genetic changes (i.e. mutations), which have been elaborately reviewed in Feyereisen et al. 2015. Mutations in the coding sequence of target-sites are the most studied toxicodynamic resistance mechanisms and the same or similar mutation can independently occur in different populations of a species distributed worldwide (e.g., *T. urticae*; Van Leeuwen et al. 2020) but also in distantly related species (e.g., *kdr* mutation; Feyereisen et al. 2015). This phenomenon has been explained as a consequence of the very limited spectrum of target-site mutations that, due to functional constraints, are allowed on conserved insecticides target-sites (Ffrench-Constant 2013; Ffrench-Constant et al. 1998). Target-site mutations are usually strongly associated with the resistance phenotype and easily detected through standard molecular biology techniques, and are considered as the best candidate for developing a molecular marker for resistance monitoring (Van Leeuwen et al. 2020). Validated molecular markers are considered to gain a central role in resistance monitoring in the future. They allow to easily assess the resistance status of a high number of individuals or even populations, overcoming the classical procedure based on toxicity tests and providing a clear picture of susceptibility in specific geographic areas (Van Leeuwen et al. 2020).

4 Target-site resistance

Surprisingly, despite the economic importance of thrips, the elucidation of target-site mutations associated with resistance has not kept pace with other main insect and mite pests. This might in part be due to the lack of genomic data until recently (Guo et al. 2020a; Rotenberg et al. 2020), impeding the relatively straightforward screening of mutations at the DNA level. Nevertheless, at present, resistance associated mutations have been identified in six target-site genes of different thrips species (Table 3).

4.1 Mutations in the voltage-gated sodium channel (VGSC)

Mutations in the VGSC have been frequently associated with pyrethroid resistance in many insect pests (Dong et al. 2014; Feyereisen et al. 2015). The well-known *kdr* mutation (L1014F, *Musca domestica* numbering) in *F. occidentalis* was uncovered as the first target-site mutation associated

Table 3. Overview of studies reporting target-site resistance mechanisms in thrips species.

MoA	Pesticide	Species	Target-site	Mutations	Reference
1A/B	Carbamates/Organophosphates	*F. occidentalis*	AChE1	A201S	This study
1A/B	Carbamates/Organophosphates	*T. tabaci*	AChE1	A201S, F290I/V, Y330F	This study
2A	Cyclodienes	*F. occidentalis*	Rdl	A301S, V327I	Meng et al. 2018
3A	Pyrethroids	*F. occidentalis*	VGSC	L1014F, T929C/V/I	Forcioli et al. 2002
3A	Pyrethroids	*T. tabaci*	VGSC	L1014F, M918T, T929I	Toda & Morishita 2009
3A	Pyrethroids	*T. palmi*	VGSC	T929I	Bao & Sonoda 2012
3A	Pyrethroids	*T. tabaci*	VGSC	M918L, V1010A	Wu et al. 2014
3A	Pyrethroids	*S. dorsalis*	VGSC	L1014F, T929I,	Yokoyama et al. 2014
3A	Pyrethroids	*T. tabaci*	VGSC	T929I, M827I, A1215D	Bao et al. 2014a
3A	Pyrethroids	*T. tabaci*	VGSC	T929I	Nazemi et al. 2016
3A	Pyrethroids	*T. tabaci*	VGSC	T929I	Aizawa et al. 2016
3A	Pyrethroids	*T. tabaci*	VGSC	T929I	Aizawa Nakai, et al. 2018
3A	Pyrethroids	*T. tabaci*	VGSC	T929I	Aizawa et al. 2018
3A	Pyrethroids	*T. tabaci*	VGSC	T929I, K1774N, M918L	Jouraku et al. 2019
3A	Pyrethroids	*T. tabaci*	VGSC	T929I, M918L	Adesanya et al. 2020
3A	Pyrethroids	*F. occidentalis*	VGSC	L1014F, T929V/I	Mavridis et al. 2022
5	Spinosyns	*F. occidentalis*	nAChR α6	G275E	Puinean et al. 2013
5	Spinosyns	*T. palmi*	nAChR α6	G275E	Bao et al. 2014b
5	Spinosyns	*F. intonsa*	nAChR α6	G275V	Hiruta et al. 2018
5	Spinosyns	*F. occidentalis*	nAChR α6	Truncated nAChR	Wan et al. 2018
5	Spinosyns	*T. palmi*	nAChR α6	G275E	Shi et al. 2021
5	Spinosyns	*F. occidentalis*	nAChR α6	G275E	Chen et al. 2021
5	Spinosyns	*F. occidentalis*	nAChR α6	G275E	Sun et al. 2022
5	Spinosyns	*F. occidentalis*	nAChR α6	G275E	Mavridis et al. 2022
6	Avermectins, Milbemycins	*F. occidentalis*	GluClc	A152D, V211E, A241T, Q344R	Gao et al. 2022
15	Benzoylureas	*F. occidentalis*	CHS-1	I1017M	Suzuki et al. 2017
15	Benzoylureas	*F. occidentalis*	CHS-1	I1017M	Mavridis et al. 2022

with pyrethroid resistance in any thrips species (Forcioli et al. 2002). The combination of the super-*kdr* mutation (M918T) with L1014F has been identified in strongly pyrethroid resistant strains of *T. tabaci* from Japan (Toda & Morishita 2009). The T929I substitution, initially associated with moderately resistant strains (Toda & Morishita 2009), has subsequently been proposed as a major factor contributing to deltamethrin resistance in Iranian *T. tabaci* populations (Nazemi et al. 2016) and cypermethrin resistance in Japan (Aizawa et al. 2016, 2018). In 2014, both L1014F and T929I were identified in a pyrethroid resistant *Scirtothrips dorsalis* population (Yokoyama et al. 2014) and, recently, in several *F. occidentalis* populations sampled in Crete (Mavridis et al. 2022). The T929I mutation might also be the main cause of the replacement of thelytokous *T. tabaci* populations with arrhenotokous ones in Japan. This could be due to a possible fitness cost of thelytokous individuals carrying the T929I mutation, which exhibits reduced biotic performance compared to arrhenotokous individuals with the T929I substitution or thelytokous individuals without the resistance mutation (Aizawa et al. 2016, 2018). Of particular note, L1014F, M918T and T929I are well-known VGSC mutations associated with pyrethroid resistance in many species, and their role has been functionally validated with electrophysiology using *Xenopus* oocytes (Rinkevich et al. 2013).

In *T. tabaci*, T929I was found coupled with a newly identified substitution K1774N in some populations, which has been proposed to enhance the effect of T929I on the VGSC in highly-resistant individuals (Jouraku et al. 2019). However, this is yet to be validated. Analysis of the complete sodium channel sequence of *T. palmi* also identified the mutations M827I and A1215D associated with T929I in strains with moderate levels of resistance to cypermethrin (Bao et al. 2014a). M827I and A1215D have previously been identified in the VGSC of *Pediculus humanus capitis* and *T. urticae,* respectively (Lee et al. 2010; Riga et al. 2017). As in *T. palmi*, the A1215D mutation in *T. urticae* always co-occurs with others VGSC mutations in resistant strains and the combination might lead to a different resistant phenotype. However, the mutation was also found fixed in some pyrethroid susceptible strains, indicating that it is not sufficient to confer the resistant phenotype (Riga et al. 2017). On the other hand, the effect of M827I mutation in reducing pyrethroid sensitivity of the VGSC has been validated in *Xenopus* oocytes (Lee et al. 2010). Last, an alternative super-*kdr* mutation (M918L), has been identified in pyrethroid-resistant *T. tabaci* populations (Adesanya et al. 2020; Jouraku et al. 2019; Wu et al. 2014). Wu and colleagues found that this mutation was always associated with a V1010A mutation (Wu et al. 2014). Whereas M918L has previously been associated with resistance in numerous insect pests (Rinkevich et al. 2013), this was the first report of V1010A, with the exception of a substitution in the same position (V1010L) described by Singh et al. (2010) for *Anopheles culicifacies.*

4.2 Mutations in the nicotinic acetylcholine receptor (nAChR)

The nAChR α6 subunit is the target of insecticidal spinosyns that comprise the compound mixtures spinosad and spinetoram, which are widely used in thrips control (Table 1). Investigations of the resistance mechanisms to spinosyns lead to the identification of a G275E substitution (numbering according to *F. occidentalis*) in the nAChR α6 subunit of spinosad-resistant *F. occidentalis* (Puinean et al. 2013). Due to the difficulty of expressing insects nAChR subunits in heterologous systems, Puinean and colleagues, expressed the closely related human nAChR α7 subunit in *Xenopus* oocytes. With this experimental setup, the G257E mutation resulted in abolishment of the modulation of the receptor mediated by spinosad (Puinean et al. 2013). The same mutation has also been associated with resistance in *T. palmi* (Bao et al. 2014b), and more recently it has been found in nine *F. occidentalis* populations from Crete, Greece (Mavridis et al. 2022). Recent studies demonstrated a high association between G275E and the expansion of *F. occidentalis* and *T. palmi* resistant populations in China and Australia (Chen et al. 2021; Shi et al. 2021; Sun et al. 2022). Therefore, G275E has been proposed as a major factor conferring resistance to spinosyns (Chen et al. 2021; Shi et al. 2021). The G275E mutation has also been described in *Tuta absoluta* strains resistant to spinosad (Silva et al. 2016) and its role in resistance has been further demonstrated by CRISPR/Cas9 editing of the α6 subunit of *Drosophila melanogaster* and *Spodoptera exigua,* resulting in an increased level of resistance (Zimmer et al. 2016; Zuo et al. 2022). Recently, functional heterologous expression of insects nAChRs has been enabled by co-expressing chaperone proteins (Hawkins et al. 2022; Rufener et al. 2020). This successful approach might pave the way toward a more fundamental understanding of insects nAChRs. It will also allow to validate mutations in the native nAChRs of a given thrips species, including the above mentioned G275E mutation as well as a recently reported G275V mutation that has been identified in a spinosad resistant strain of *F. intonsa* (Hiruta et al. 2018). Last, in addition to mutations interfering with binding, disruption of nAChRs has been demonstrated as a common mechanism of resistance to spinosyns in several insect species (Wang et al. 2020a). Target-site disruption is a rare resistance mechanism in arthropods, and is probably only possible because of the functional redundancy between some of the alfa subunits (Feyereisen et al. 2015). In *F. occidentalis*, the truncated nAChR α6 subunit (Foccα6), caused by alternative splicing, has been positively correlated with spinosad resistance (Wan et al. 2018). Null mutations on *Dmα6* of *D. melanogaster* confer even higher level of resistance compared to the G275E mutation (Zimmer et al. 2016) and the effect of truncated nAChR α6 on spinosyn resistance has also been confirmed for other insect species, including *S. exigua, S. frugiperda* and *Helicoverpa armigera*, for which it was shown that CRISPR/Cas9 knockout of the nAChR α6 leads to a considerable increment of resistance to spinosyns (Fig. 3; Shi et al. 2022; Wang et al. 2020a; Zuo et al. 2020).

4.3 Mutations in chitin synthase 1 (CHS-1)

CHS-1 is a crucial enzyme involved in chitin biosynthesis in arthropods. In 2012, Van Leeuwen and colleagues used a high-resolution population level bulked segregant analysis to map a case of monogenic etoxazole resistance to a single genomic locus, coinciding with CHS-1. Further genetic and biochemical evidence supported a mutation in the fifth transmembrane domain (TM5) of the CHS-1 gene, I1017F as the causal resistance mutation, hereby also resolving the mode of action of this class of compounds (Demaeght et al. 2014; Van Leeuwen et al. 2012). In a follow-up study, it was revealed that a mutation at the same site (I1017M) was strongly associated with resistance to the insecticide classes of benzoylureas and buprofezin in *Plutella xylostella* (Douris et al. 2016). In the same study, the role of the I1017F/M mutation in resistance was functionally validated with CRISPR/Cas9-editing of the CHS-1 gene in *D. melanogaster* (Douris et al. 2016). The I1017F mutation was also identified as a major factor in diflubenzuron and etoxazole resistance in *Culex pipiens* and *Panonychus citri*, respectively (Fotakis et al. 2020; Tadatsu et al. 2022). In 2017, it was also shown that a benzoylurea-resistant *F. occidentalis* population from Japan carried the I1017M mutation (Suzuki et al. 2017) while in 2022, I1017M was detected in multiple *F. occidentalis* populations from Crete (Mavridis et al. 2022). More recently, a bulk-segregant mapping method was also used to investigate buprofezin resistance in the brown planthopper *Nilaparvata lugens* and a new mutation in TM1 of CHS-1, G932C, was identified and functionally validated using CRISPR/Cas9-editing of CHS-1 in *D. melanogaster* (Zeng et al. 2022). Hence, one might consider to screen both the TM1 and TM5

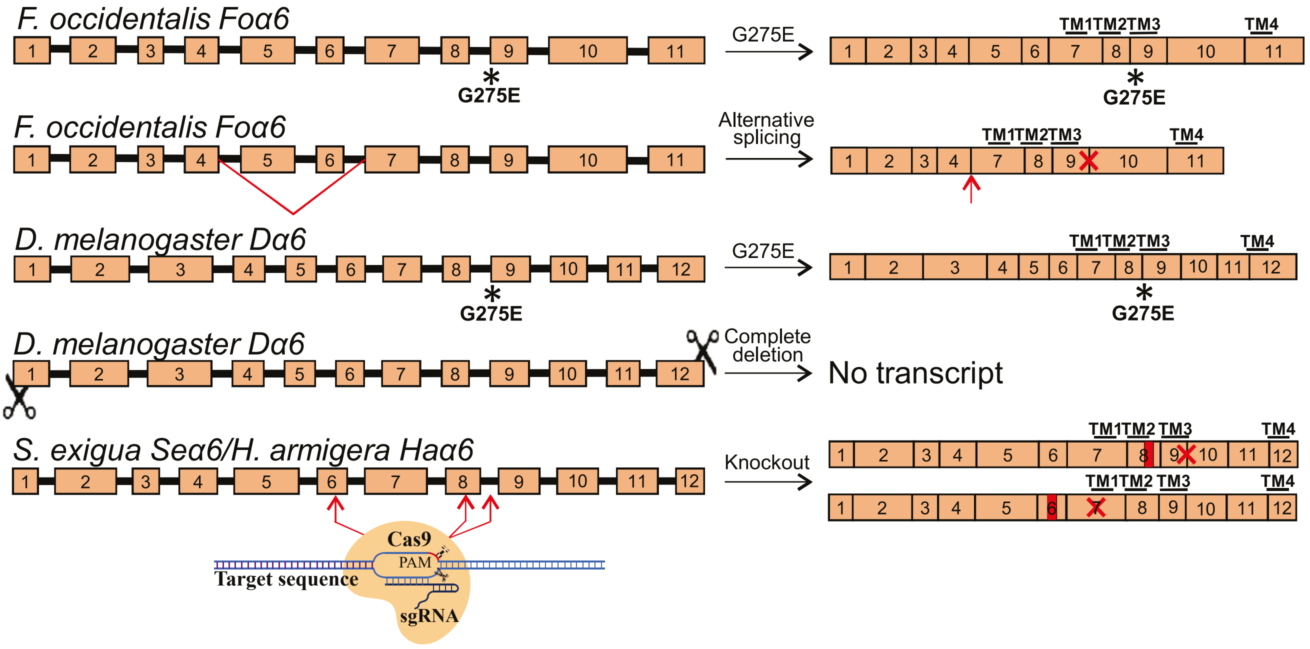

Fig. 3. Schematic representation of reported genetic mechanism of spinosad resistance. Gene exons of nAChR are represented by orange numbered boxes. Conserved transmembrane (TM) domains are indicated with black lines in all transcripts. Asterisks indicate the position of the G275E mutation in *F. occidentalis* and *D. melanogaster* gene/transcript. Red crosses indicate the position of protein disruption, resulting in loss of function. Scissors at both ends of *Dmα6* indicate the complete lack of *Dmα6* due to a chromosome deletion in a commercial *Dmα6*-deficient *D. melanogaster* strain. Red arrows indicate the position of alternative splicing in *Foα6* and the target region of Cas9 on *Seα6* and *Haα6* while indels are represented with red rectangles on transcripts.

regions of CHS-1 for the presence of mutations in future screening studies of resistant thrips populations.

4.4 Mutations in glutamate-gated chloride channel (GluCl)

GluCl is considered as the main target-site of macrocyclic lactone insecticides (Wolstenholme 2012). Most insects have only one GluCl gene, but alternative splicing and RNA editing result in the necessary functional variation of these channels (Dermauw et al. 2012; Wolstenholme 2012). Recently, two GluCl genes have been found in *Blattella germanica* and *Periplaneta americana* (Jones et al. 2021) and surprisingly, six GluCl genes have been identified in the spider mite *T. urticae* (Dermauw et al. 2012). Several mutations in GluCl genes have been associated with macrocyclic resistance in both insect and mite species and have also been functionally validated (Dermauw et al. 2012; Mermans et al. 2017; Wang et al. 2017; Xue et al. 2021). In *F. occidentalis* and *F. intonsa* three GluCl genes – *FoGluCla, FoGluClb* and *FoGluClc* – have been identified, with *FoGluClc* showing low similarity with the other GluCls, but sharing functionally important loops and the possibility to form a homopentamer (Gao et al. 2022). The sequence and the expression level of *FoGluCla, FoGluClb* and *FoGluClc* have been compared between an emamectin benzoate (EB)-susceptible and EB-resistant strains (Gao et al. 2022). No substitution was found in *FoGluCla* and *FoGluClb* and no significant differences could be observed in their expression levels. However, *FoGluClc* of the resistant population carried the A152D, V211E, A241T and Q344R mutations and this GluCl was significantly overexpressed in the resistant strain. Of particular note, these amino acid substitutions were also present in *FoGluClc* of a Hawaiian field-collected strain that was used for sequencing of the complete *F. occidentalis* genome (Rotenberg et al. 2020), suggesting these putative resistance alleles are relatively common in the field (Gao et al. 2022).

4.5 Mutations in γ-aminobutyric acid (GABA)-gated chloride channel (Rdl)

The Rdl (Resistance to dieldrin) channel is the target-site of cyclodienes and phenylpyrazole (class 2A and 2B respectively according to IRAC MoA classification) and mutations in *Rdl* conferring resistance to cyclodienes (e.g. dieldrin) and/or phenylpyrazole (e.g. fipronil) have been frequently reported for insects (Ffrench-Constant et al. 1993; Sheng et al. 2018; Wondji et al. 2011). The A301S (*D. melanogaster* numbering) and V327I (*Anopheles* species numbering) mutations, previously associated with cyclodiene resistance in other insect species (Ffrench-Constant et al. 1993; Sheng et al. 2018; Wondji et al. 2011), were detected in two *F. occi-*

dentalis strains (Meng et al. 2018). However, whether these mutations confer cyclodiene resistance in the two strains was not investigated with bioassays, but their presence might reflect the strong selective pressure of cyclodienes in the past (Meng et al. 2018). Peculiarly, analysis of the *Rdl* sequence of the *F. occidentalis* strain utilized for genome sequencing (Rotenberg et al. 2020) also revealed the presence of A301S and V327I mutations (NCBI accession XP_052123188.1).

4.6 Mutations in acetylcholine esterase (AChE)

AChE is the target-site of carbamates and organophosphates (OPs), two classes of insecticides that have been broadly used against many thrips species around the world (Table 1). Like most insects, thrips species have two AChEs (AChE1 and AChE2) whereas higher Diptera have only one and, except for Cyclorrhapha, AchE1 seems to be the main catalytic enzyme in most insects (Feyereisen et al. 2015; Kim & Lee 2013; Rotenberg et al. 2020). Resistance to both carbamates and OPs has been reported in thrips (Adesanya et al. 2020; Lebedev et al. 2013; Nazemi et al. 2016; Negash et al. 2021). Target-site mutations in AChE associated with resistance are frequently reported in numerous arthropod species (Fig. S1; Andrews et al. 2004; Vontas et al. 2002; Weill et al. 2004). Although previous studies suggested that AChE insensitivity plays a major role in thrips resistance against carbamates and OPs, investigations into the molecular determinants were not performed and, consequently, AChE mutations have not yet been reported for resistant thrips populations. (Adesanya et al. 2020; Nazemi et al. 2016; Zhao et al. 1994). In this review, we performed an exploratory analysis on a limited set of thrips sequencing data available in public databases and screened for the presence of mutations at AChE positions for which resistance mutations have been frequently reported in other metazoan species: G119, A201, F290, Y330 and F331 (*Torpedo californica* numbering; Lenfant et al. 2013). Phylogenetic constraints, such as reported for OPs in mosquito AChEs (Weill et al. 2004), seems not the reason of their absence, as single nucleotide substitutions could result in previously documented resistance mutations in thrips AChE1 or AChE2 (Table S2, File S1). To our surprise, we did identify an A201S, F290I/V and Y330F mutation in AChE1 of *T. tabaci* populations (based on SRA accessions DRR157291, DRR157303/DRR157291 and DRR157288, respectively; see File S2), while an A201S mutation was found in AChE1 of two *F. occidentalis* populations (based on SRA accession SRR17407430 and the *F. occidentalis* genome; see File S2). Both A201S and F290V have previously been strongly associated with resistance in many arthropod species (Cassanelli et al. 2006; Guan et al. 2021; İnak 2022; Lenfant et al. 2013; Simma et al. 2020), while an Y330F mutation was shown to increase sensitivity to OPs in *D. melanogaster* AChE2 (Villatte et al. 1998). The presence of these mutations might reflect the recent or historical use of carbamates and OPs to control thrips populations.

5 Metabolic resistance

The detoxification process comprises three phases: (i) phase I enzymes including P450s and carboxyl/cholinesterases (CCEs) convert toxic molecules into more hydrophilic and reactive compounds that are (ii) conjugated with endogenous molecules by phase II enzymes such as glutathione S-transferases (GSTs) and UDP-glycosyltransferases (UGTs) while, finally, in phase III (iii) cellular transporters, such as ABC transporters move toxicants out of the cells for excretion or sequestration (Ahn et al. 2021; Dermauw et al. 2020; Dermauw & Van Leeuwen 2014; Pavlidi et al. 2018). More recently, other players in metabolism have also been associated with xenobiotic resistance in insect and mite species, which include members of the Major Facilitator Transporter superfamily, short chain reductases and intradiol-ring cleavage dioxygenases (Njiru et al. 2022; Snoeck et al. 2017, 2018). All these enzyme families are involved in several endogenous processes, but also in resistance via increased metabolism and transport of xenobiotic molecules (Kennedy & Tierney 2013; Van Leeuwen & Dermauw 2016). It is often argued that highly polyphagous insects, including the main thrips species, are equipped with a more developed detoxification tool-kit to resist the wide array of plant defense molecules, when compared to monophagous specialist insects (Rane et al. 2016, 2019). This so called 'pre-adaptation syndrome' might allow to better resist synthetic pesticides, and lead to rapid resistance development (Dermauw et al. 2018; Rane et al. 2016, 2019). Although this hypothesis might seem supported by the fact that more resistance cases have been reported for polyphagous pests compared to monophagous ones (Crossley et al. 2021; Rane et al. 2016, 2019), this correlation might also reflect the economic importance of polyphagous pests and therefore the selective pressure imposed by the more frequent use of pesticides necessary for their control (Dermauw et al. 2018). Nonetheless, the molecular basis of host plant adaptation and development of insecticide resistance largely overlap. For spider mites, similar transcriptional detoxification responses have been observed after pesticide selection and adaptation or acclimatization to a new host plant (Dermauw et al. 2013b; Wybouw et al. 2019). Not surprisingly, in *F. occidentalis* the observed rapid change in expression of detoxification genes is associated with both adaptation to new challenging hosts (Yue et al. 2022), and different pesticide treatments (Gao et al. 2020).

6 What we learned from classical biochemical tools and assays

General enzyme activity assays together with synergism studies have been the main tools to investigate the role of detoxification enzymes in thrips resistance. In these studies, the involvement of metabolism as a resistance factor is mostly implied via a simple correlation of higher enzyme activity, determined with model substrates, in a particular resistant population compared to a susceptible (laboratory reference) population (Badieinia et al. 2020; Fu et al. 2019; Herron et al. 2014; Jensen 1998; Thalavaisundaram et al. 2012). More evidence for causality is derived from synergism studies that exploit inhibitors of detoxification enzymes to examine the role of specific enzyme families in resistance by monitoring differences in resistance ratio in presence and absence of the inhibitor in both susceptible and resistant strains (Bernard & Philogène 1993; Snoeck et al. 2017). These studies are relatively time-consuming and require an adequate number of insects which often implies that populations need to be established in the laboratory. But more importantly, they do not provide any information on the genetic bases underlying metabolic resistance and these assays rarely lead to the discovery of diagnostic markers that can be used for resistance management purpose (Van Leeuwen et al. 2020). Nevertheless, for the majority of the recently reported thrips resistance cases, resistance has been associated with an increased activity of general detoxification enzymes using the classic methods described above (Gao et al. 2012). The studies investigating metabolic resistance in thrips are summarized in Table 4. P450s seems to have the main role in detoxification, as their enhanced activity has often been indicated as highly associated with resistance to several classes of pesticides (Adesanya et al. 2020; Bao et al. 2015; Bao et al. 2014b; Bao & Sonoda 2012; Chen et al. 2011; Espinosa et al. 2005; Gao et al. 2014). An increased activity of GSTs and CCEs has also been correlated with resistance, either in concert with P450s (Adesanya et al. 2020; Fu et al. 2019; Gao et al. 2014; Wang et al. 2012), or occasionally as main mechanism, even though this might be the result of the focus of researchers on a single mechanism (Gholami et al. 2020; Herron et al. 2014; Jensen 1998; Thalavaisundaram et al. 2012). Last, some members of the CCE family have been reported to protect against toxic substances by sequestration (Pittendrigh et al. 2014) and such resistance mechanism has also been proposed for *F. occidentalis* in the case of spinosad resistance (Herron et al. 2014).

7 The rapid progress in the genomic era

During the last decade, the RNA sequencing technology has been frequently used to quantify transcripts levels on a genome wide scale and has also been used to elucidate candidate resistance genes involved in metabolic resistance. In the case of thrips, P450s have been observed as highly upregulated in a spinosad-resistant *T. tabaci* population (Rosen et al. 2021) and several P450s were also highly expressed in a *T. tabaci* strain resistant to spinetoram (Guo et al. 2020a). Three overexpressed CYP genes (*Cyp3659A1, Cyp6EB2* and *Cyp6EC1*) were also suggested as causal candidate genes in emamectin benzoate resistance in *F. occidentalis* (Gao et al. 2022). Interestingly, overexpression of *Cyp6EC1* and *Cyp6EB1* has previously also been associated with acrinathrin resistance in *F. occidentalis* (Cifuentes et al. 2012), but without functional validation.

Next to P450s, the overexpression of enzymes or transporters that are known to be involved in detoxification have also been reported for *Frankliniella* and *Thrips* populations. UGTs are conjugation enzymes that have been previously associated with insecticide resistance (Ahn et al. 2021; Bock 2016; Li et al. 2017) and four UGT genes were overexpressed after treatment of *F. occidentalis* with sublethal doses of different pesticides (Gao et al. 2020). ATP-binding cassette (ABC) transporters can export toxic compounds from the cell and have been associated with insecticide resistance in many arthropods (Dermauw & Van Leeuwen 2014). In 2020, a transcriptomic study revealed that a gene of the ABCG subfamily, was upregulated in *F. occidentalis* after pesticide treatment, suggesting the involvement of this transporter in insecticide responses (Gao et al. 2020). In contrast, some ABC genes were downregulated in a spinetoram resistant *T. palmi* population compared to a susceptible one (Guo et al. 2020a), indicating that transcriptomic studies alone might not be predictive of the role of ABC transporters in thrips resistance and cases must always be functionally validated.

Noteworthy, even when a correlation between the expression of a resistance gene and resistance levels can be made, the genetic basis of the increased expression remains elusive. The identification of resistance-associated mutations in cis- and trans-elements that regulate expression of detoxification enzymes could allow to easily screen large populations for resistance and could consequently lead to effective resistance management programs (Van Leeuwen et al. 2020). Recently, such mutations have been identified in malaria-vector mosquitos (Mugenzi et al. 2019; Weedall et al. 2019) and T. urticae (Fotoukkiaii et al. 2021; Kurlovs et al. 2022; Papapostolou et al. 2022), although no studies have been performed in thrips species yet. At least in the case of the spider mite *T. urticae*, it is clear that trans regulation of detoxification enzymes is abundant, suggesting a modular control of gene expression, which is particularly clear for P450s (Kurlovs et al. 2022).

8 What can we learn from recently sequenced thrips genomes?

In 2019, the genome of the oligophagous thrips species *Aptinotrips rufus* (GenBank accession GCA_902196195.1) was deposited in the NCBI database, while the genome of two polyphagous thrips species, *F. occidentalis* and *T. palmi*, were published in 2020. The genome size of these three species was between 238 and 416 Mbp. Especially

Table 4. Overview of studies reporting metabolic resistance mechanisms in thrips species since 2012.

MoA	Pesticide	Species	Enzymes	Evidence	Genes	Reference
1A	Oxamyl	*T. tabaci*	P450s/CCEs	Enzyme kinetics	Unknown	Adesanya et al. 2020
1A	Methomyl	*T. tabaci*	P450s/CCEs	Enzyme kinetics	Unknown	Adesanya et al. 2020
1B	Phoxim	*F. occidentalis*	P450s/CCEs	Enzyme kinetics/ Synergism	Unknown	Wang et al. 2012
1B	Chlorpyrifos	*F. occidentalis*	P450	Proteomic analysis	CYP6-like	Yan et al. 2015
1B	Profenofos	*T. tabaci*	P450s	Synergism	Unknown	Nazemi et al. 2016
1B	Dichlorvos	*F. occidentalis*	CCEs/GSTs	Enzyme kinetics/ Synergism	Unknown	Gholami et al. 2020
3	Acrinathrin	*F. occidentalis*	P450S	Expression analysis	*CYP6EB1*, *CYP6EC1*	Cifuentes et al. 2012
3	Cypermethrin	*T. palmi*	P450s	Synergism	Unknown	Bao & Sonoda 2012
3	tau-Fluvalinate	*F. occidentalis*	CCEs/GSTs	Enzyme kinetics	Unknown	Thalavaisundaram et al. 2012
3	Deltamethrin	*T. tabaci*	P450s/GSTs	Synergism	Unknown	Nazemi et al. 2016
4	Acetamiprid	*F. occidentalis*	P450s	Synergism	Unknown	Minakuchi et al. 2013
4	Thiamethoxam	*F. occidentalis*	P450s/CCEs	Enzyme kinetics/ Synergism	Unknown	Gao et al. 2014
4	Imidacloprid	*T. hawaiiensis*	P450s/CCEs/GSTs	Enzyme kinetics/ Synergism	Unknown	Fu et al. 2019
5	Spinosad	*F. occidentalis*	CCEs	Enzyme kinetics/ Synergism	Unknown	Herron et al. 2014
5	Spinosad	*T. palmi*	P450s	Synergism	Unknown	Bao et al. 2014b
5	Imidacloprid	*T. palmi*	P450s	Synergism	Unknown	Bao et al. 2015
5	Spinetoram	*T. hawaiiensis*	P450s	Enzyme kinetics/ Synergism	Unknown	Fu et al. 2019
5	Spinetoram	*T. tabaci*	P450s	Transcriptomic analysis	Multiple CYPs	Guo et al. 2020b
5	Spinosad	*T. tabaci*	P450s	Transcriptomic analysis	CYP4g15-like, *CYP4C39*	Rosen et al. 2021
6	Abamectin	*T. hawaiiensis*	P450s/CCEs/GSTs	Enzyme kinetics/ Synergism	Unknown	Fu et al. 2019
6	Abamectin	*T. tabaci*	P450s/CCEs	Enzyme kinetics	Unknown	Adesanya et al. 2020
6	Emamectin benzoate	*F. occidentalis*	P450s	Synergism/Transcriptomic analysis	*Cyp3659A1*, *Cyp6EB2*, *Cyp6EC1*	Gao et al. 2022
UN	Pyridalyl	*F. occidentalis*	P450s/GSTs	Synergism	Unknown	Wang et al. 2020b

the genome assembly of *T. palmi* was of high quality as it consisted of only 17 scaffolds. We took advantage of the deposited genome sequences to annotate for the first time the GST gene family in *F. occidentalis* and to correct the previous GST annotation proposed for *T. palmi*. Genes encoding detoxification enzymes – CYPs, GSTs, CCEs and UGTs – and ABC transporters, are now completely annotated for both *F. occidentalis* and *T. palmi* (Guo et al. 2020b; Rotenberg et al. 2020; this study, Table 5). The number of predicted UGT genes for these two thrips species is lower than other polyphagous insects (Guo et al. 2020b). The number of GSTs, on the other hand, is similar to other insects but a relatively higher number of sigma GSTs – reported to play a role in stress tolerance (Hassan et al. 2019; Zhang et al. 2022b) – is present in *F. occidentalis*. Both thrips species have between 96 and 112 CYP genes, which is higher than the CYP number reported for aphids (Chertemps et al. 2021) but lower than those found in the genome of the whitefly *Bemisia tabaci*, another polyphagous herbivore within the Condylognatha (= Hemiptera + Thysanoptera; Chen et al. 2016). As in most insect CYPomes, the CYP4 and CYP3 clan were overrepresented, and a phylogenetic analysis revealed thrips-specific expansions in the CYP4 clan of both thrips species. Further, the two thrips species have relatively more

Table 5. Number of detoxification genes (CYPs, CCEs, GSTs, UGTs) and ABC transporters in *F. occidentalis, T. palmi* and other members of the Condylognatha, including the whitefly *B. tabaci* and the pea aphid *A. pisum*.

	subfamily/clan	***F. occidentalis***	***T. palmi***	***B. tabaci* (MEAM1)**	***A. pisum***
CYP	Clan2	12[a]	11[b]	10[c]	10[f]
	Clan3	30[a]	21[b]	57[c]	23[f]
	Clan4	57[a]	49[b]	56[c]	23[f]
	Mito	13[a]	15[b]	7	8[f]
	Total	112[a]	96[b]	130[c]	64[f]
CCE	Total	50[a]	39[b]	51[c]	31[f]
GST (cytosolic)	GST delta/GST epsilon	9[g]	(14[b]) 16[g]	12[d]	11[f]
	GST sigma	8[g]	(6[b]) 4[g]	6[d]	5[f]
	GST omega	1[g]	(1[b]) 1[g]	0[d]	2[f]
	GST theta	1[g]	(1[b]) 1[g]	1[d]	2[f]
	GST zeta	2[g]	(2[b]) 1[g]	2[d]	2[f]
	GST unknown	0[g]	(0[b]) 0[g]	0[d]	1[f]
	Total	21[g]	(24[b]) 23[g]	21[d]	23[f]
UGT	Total	17[b]	17[b]	76[e]	55[f]
ABC	ABCB	5[a]	4[b]	4[c]	9[f]
	ABCC	11[a]	12[b]	6[c]	16[f]
	ABCG	14[a]	16[b]	16[c]	19[f]
	ABCH	6*[a]	7[b]	9[c]	9[f]
	ABC-other	9[a]	10[b]	15[c]	18[f]
	Total	45[a]	49[b]	50[c]	71[f]

* 7 ABCH genes if the partial but conserved ABCH-06 would be included

[a] Rotenberg et al. 2020

[b] Guo et al. 2020b

[c] Chen et al. 2016

[d] He et al. 2018

[e] Guo et al. 2020a

[f] Chertemps et al. 2021

[g] This study; phylogenetic tree in supplementary Fig. S2/File S3

CCE genes than aphids, and the high number of CCEs in *F. occidentalis* has been attributed to a lineage-specific expansion within the dietary/detoxification class of CCEs (Table 5; Guo et al. 2020a; Rotenberg et al. 2020; Xie et al. 2018). Future research should focus on whether the rapid development of insecticide resistance of *F. occidentalis* and *T. palmi* might be related to the observed CYP4 expansions and the high number of CCE genes in both thrips species. Last, a lineage-specific expansion of ABCH gene family, of which some members are known to respond to xenobiotic exposure in other species (Bryon et al. 2013; Dermauw et al. 2013a; Qi et al. 2016), has been identified in *F. occidentalis* (Guo et al. 2020a; Rotenberg et al. 2020). However, such ABCH expansions have also been reported in Hemiptera and the spider mite *T. urticae* (Denecke et al. 2021; Dermauw et al. 2013a; Table 5) and the role of ABCHs in insecticide resistance remains to be functionally validated. In addition to easing the identification of key enzymes or transporters involved in resistance (e.g., the above mentioned *FoGluClc* gene only present in *Frankliniella* species; Gao et al. 2022), both thrips genomes will also allow to more easily screen for target-site resistance mutations at the DNA level (e.g., by Sanger sequencing or droplet digital (dd)PCR), and might facilitate the use of molecular markers in resistance management programs (Van Leeuwen et al. 2020). For example, Mavridis et al. recently developed and validated a ddPCR diagnostic for the main resistance mutations identified in VGSC, nAChRα6 ad CHS-1 of *F. occidentalis*. This method can be applied to bulk pooled samples and will simplify and reduce costs of diagnostics as well as provide a remarkable detection sensibility (Mavridis et al. 2022). Further, the available thrips genomes will facilitate transcriptomic studies (using the genome as a mapping reference) and will permit to perform high resolution genetic mapping (QTL mapping), for example with a bulked segregant analyses, which could aid in the unbiased identification of new resistance mechanisms and/or target-sites of insecticides (Fotoukkiaii et al. 2021; Kurlovs et al. 2019; Wybouw et al. 2019). Finally, thrips genomes will also be essential for tailoring the CRISPR/Cas9 technique to thrips species (e.g. for the design of sgRNAs), which could be useful for the investigation of key detoxification or transporter genes and the validation of target-site mutations.

During the proofing stage, an insertion in intron 3 of *nAChRα6* was reported as another thrips resistance mechanism against spinosad (https://doi.org/10.1127/entomologia/2022/1733; see Figure 3).

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References

Adesanya, A. W., Waters, T. D., Lavine, M. D., Walsh, D. B., Lavine, L. C., & Zhu, F. (2020). Multiple insecticide resistance in onion thrips populations from Western USA. *Pesticide Biochemistry and Physiology, 165*, 104553. https://doi.org/10.1016/j.pestbp.2020.104553

Ahn, S.-J., Chertemps, T., Maïbèche, M., Marygold, S. J., & Van Leeuwen, T. (2021). Editorial: Invertebrate UDP-glycosyltransferases: nomenclature, diversity and functions. *Frontiers in Physiology, 12*, 748290. https://doi.org/10.3389/fphys.2021.748290

Aizawa, M., Watanabe, T., Kumano, A., Miyatake, T., & Sonoda, S. (2016). Cypermethrin resistance and reproductive types in onion thrips, Thrips tabaci (Thysanoptera: Thripidae). *Journal of Pesticide Science, 41*(4), 167–170. https://doi.org/10.1584/jpestics.D16-049

Aizawa, M., Watanabe, T., Kumano, A., Tamagaki, K., & Sonoda, S. (2018). Biotic performances of thelytokous and arrhenotokous strains of Thrips tabaci (Thysanoptera: Thripidae) showing resistance to cypermethrin. *Applied Entomology and Zoology, 53*(1), 11–17. https://doi.org/10.1007/s13355-017-0522-z

Andrews, M. C., Callaghan, A., Field, L. M., Williamson, M. S., & Moores, G. D. (2004). Identification of mutations conferring insecticide-insensitive AChE in the cotton-melon aphid, Aphis gossypii Glover. *Insect Molecular Biology, 13*(5), 555–561. https://doi.org/10.1111/j.0962-1075.2004.00517.x

Arakaki, N., Miyoshi, T., & Noda, H. (2001). *Wolbachia*– mediated parthenogenesis in the predatory thrips *Franklinothrips vespiformis* (Thysanoptera: Insecta). *Proceedings. Biological Sciences, 268*(1471), 1011–1016. https://doi.org/10.1098/rspb.2001.1628

Badieinia, F., Khajehali, J., Nauen, R., Dermauw, W., & Van Leeuwen, T. (2020). Metabolic mechanisms of resistance to spirodiclofen and spiromesifen in Iranian populations of Panonychus ulmi. *Crop Protection (Guildford, Surrey), 134*, 105166. https://doi.org/10.1016/j.cropro.2020.105166

Balabanidou, V., Grigoraki, L., & Vontas, J. (2018). Insect cuticle: A critical determinant of insecticide resistance. *Current Opinion in Insect Science, 27*, 68–74. https://doi.org/10.1016/j.cois.2018.03.001

Bao, W. X., & Sonoda, S. (2012). Resistance to cypermethrin in melon thrips, Thrips palmi (Thysanoptera: Thripidae), is conferred by reduced sensitivity of the sodium channel and CYP450-mediated detoxification. *Applied Entomology and Zoology, 47*(4), 443–448. https://doi.org/10.1007/s13355-012-0141-7

Bao, W. X., Kataoka, Y., Fukada, K., & Sonoda, S. (2015). Imidacloprid resistance of melon thrips, *Thrips palmi*, is conferred by CYP450-mediated detoxification. *Journal of Pesticide Science, 40*(2), 65–68. https://doi.org/10.1584/jpestics.D15-004

Bao, W. X., Kataoka, Y., Kohara, Y., & Sonoda, S. (2014a). Genomic analyses of sodium channel α-subunit genes from strains of melon thrips, Thrips palmi, with different sensitivities to cypermethrin. *Pesticide Biochemistry and Physiology, 108*, 80–85. https://doi.org/10.1016/j.pestbp.2013.12.009

Bao, W. X., Narai, Y., Nakano, A., Kaneda, T., Murai, T., & Sonoda, S. (2014b). Spinosad resistance of melon thrips, Thrips palmi, is conferred by G275E mutation in α6 subunit of nicotinic acetylcholine receptor and cytochrome P450 detoxification. *Pesticide Biochemistry and Physiology, 112*, 51–55. https://doi.org/10.1016/j.pestbp.2014.04.013

Bernard, C. B., & Philogène, B. J. R. (1993). Insecticide synergists: role, importance, and perspectives. *Journal of Toxicology and Environmental Health, 38*(2), 199–223. https://doi.org/10.1080/15287399309531712

Bock, K. W. (2016). The UDP-glycosyltransferase (UGT) superfamily expressed in humans, insects and plants: Animal-plant arms-race and co-evolution. *Biochemical Pharmacology, 99*, 11–17. https://doi.org/10.1016/j.bcp.2015.10.001

Bryon, A., Wybouw, N., Dermauw, W., Tirry, L., & Van Leeuwen, T. (2013). Genome wide gene-expression analysis of facultative reproductive diapause in the two-spotted spider mite Tetranychus urticae. *BMC Genomics, 14*(1), 815. https://doi.org/10.1186/1471-2164-14-815

Cassanelli, S., Reyes, M., Rault, M., Carlo Manicardi, G., & Sauphanor, B. (2006). Acetylcholinesterase mutation in an insecticide-resistant population of the codling moth Cydia pomonella (L.). *Insect Biochemistry and Molecular Biology, 36*(8), 642–653. https://doi.org/10.1016/j.ibmb.2006.05.007

Chen, W., Hasegawa, D. K., Kaur, N., Kliot, A., Pinheiro, P. V., Luan, J., … Fei, Z. (2016). The draft genome of whitefly Bemisia tabaci MEAM1, a global crop pest, provides novel insights into virus transmission, host adaptation, and insecticide resistance. *BMC Biology, 14*(1), 110. https://doi.org/10.1186/s12915-016-0321-y

Chen, X., Yuan, L., Du, Y., Zhang, Y., & Wang, J. (2011). Cross-resistance and biochemical mechanisms of abamectin resistance in the western flower thrips, Frankliniella occidentalis. *Pesticide Biochemistry and Physiology, 101*(1), 34–38. https://doi.org/10.1016/j.pestbp.2011.07.001

Chen, Y., Nguyen, D. T., Gupta, R., & Herron, G. A. (2021). Mutation (G275E) of nAChR subunit Foα6 associated with spinetoram resistance in Australian western flower thrips, Frankliniella occidentalis (Pergande). *Molecular Biology Reports, 48*(4), 3155–3163. https://doi.org/10.1007/s11033-021-06372-3

Chertemps, T., Le Goff, G., Maïbèche, M., & Hilliou, F. (2021). Detoxification gene families in Phylloxera: Endogenous functions and roles in response to the environment. *Comparative Biochemistry and Physiology. Part D, Genomics & Proteomics, 40*, 100867. https://doi.org/10.1016/j.cbd.2021.100867

Cifuentes, D., Chynoweth, R., Guillén, J., De La Rúa, P., & Bielza, P. (2012). Novel cytochrome P450 genes, CYP6EB1 and CYP6EC1, are over-expressed in acrinathrin-resistant Frankliniella occidentalis (Thysanoptera: Thripidae). *Journal of Economic Entomology, 105*(3), 1006–1018. https://doi.org/10.1603/EC11335

Cluever, J. D., & Smith, H. A. (2017). A photo-based key of thrips (Thysanoptera) associated with horticultural crops in Florida. *The Florida Entomologist, 100*(2), 454–467. https://doi.org/10.1653/024.100.0208

Crossley, M. S., Snyder, W. E., & Hardy, N. B. (2021). Insect-plant relationships predict the speed of insecticide adaptation. *Evolutionary Applications, 14*(2), 290–296. https://doi.org/10.1111/eva.13089

Cubillos-Salamanca, Y. P., Rodríguez-Maciel, J. C., Pineda-Guillermo, S., Silva-Rojas, H. V., Berzosa, J., Tejeda-Reyes, M. A., & Rebollar-Alviter, Á. (2020). Identification of thrips species and resistance of Frankliniella occidentalis (Thysanoptera: Thripidae) to malathion, spinosad, and bifenthrin in blackberry crops. *The Florida Entomologist, 102*(4), 738–746. https://doi.org/10.1653/024.102.0411

Demaeght, P., Osborne, E. J., Odman-Naresh, J., Grbić, M., Nauen, R., Merzendorfer, H., … Van Leeuwen, T. (2014). High resolution genetic mapping uncovers chitin synthase-1 as the target-site of the structurally diverse mite growth inhibitors clofentezine, hexythiazox and etoxazole in Tetranychus urticae. *Insect Biochemistry and Molecular Biology, 51*, 52–61. https://doi.org/10.1016/j.ibmb.2014.05.004

Denecke, S., Rankić, I., Driva, O., Kalsi, M., Luong, N. B. H., Buer, B., … Vontas, J. (2021). Comparative and functional genomics of the ABC transporter superfamily across arthropods. *BMC Genomics, 22*(1), 553. https://doi.org/10.1186/s12864-021-07861-2

Dermauw, W., & Van Leeuwen, T. (2014). The ABC gene family in arthropods: Comparative genomics and role in insecticide transport and resistance. *Insect Biochemistry and Molecular Biology, 45*, 89–110. https://doi.org/10.1016/j.ibmb.2013.11.001

Dermauw, W., Ilias, A., Riga, M., Tsagkarakou, A., Grbić, M., Tirry, L., … Vontas, J. (2012). The cys-loop ligand-gated ion channel gene family of Tetranychus urticae: Implications for acaricide toxicology and a novel mutation associated with abamectin resistance. *Insect Biochemistry and Molecular Biology, 42*(7), 455–465. https://doi.org/10.1016/j.ibmb.2012.03.002

Dermauw, W., Osborne, E. J., Clark, R. M., Grbić, M., Tirry, L., & Van Leeuwen, T. (2013a). A burst of ABC genes in the genome of the polyphagous spider mite Tetranychus urticae. *BMC Genomics, 14*(1), 317. https://doi.org/10.1186/1471-2164-14-317

Dermauw, W., Pym, A., Bass, C., Van Leeuwen, T., & Feyereisen, R. (2018). Does host plant adaptation lead to pesticide resistance in generalist herbivores? *Current Opinion in Insect Science, 26*,25–33. https://doi.org/10.1016/j.cois.2018.01.001

Dermauw, W., Wybouw, N., Rombauts, S., Menten, B., Vontas, J., Grbić, M., … Van Leeuwen, T. (2013b). A link between host plant adaptation and pesticide resistance in the polyphagous spider mite Tetranychus urticae. *Proceedings of the National Academy of Sciences of the United States of America, 110*(2), E113–E122. https://doi.org/10.1073/pnas.1213214110

Dermauw, W., Van Leeuwen, T., & Feyereisen, R. (2020). Diversity and evolution of the P450 family in arthropods. *Insect Biochemistry and Molecular Biology, 127*, 103490. https://doi.org/10.1016/j.ibmb.2020.103490

Diaz-Montano, J., Fuchs, M., Nault, B. A., Fail, J., & Shelton, A. M. (2011). Onion thrips (Thysanoptera: Thripidae): a global pest of increasing concern in onion. *Journal of Economic Entomology, 104*(1), 1–13. https://doi.org/10.1603/EC10269

Ding, T., Chi, H., Gökçe, A., Gao, Y., & Zhang, B. (2018). Demographic analysis of arrhenotokous parthenogenesis and bisexual reproduction of Frankliniella occidentalis (Pergande) (Thysanoptera: Thripidae). *Scientific Reports, 8*(1), 3346. https://doi.org/10.1038/s41598-018-21689-z

Dong, K., Du, Y., Rinkevich, F., Nomura, Y., Xu, P., Wang, L., … Zhorov, B. S. (2014). Molecular biology of insect sodium channels and pyrethroid resistance. *Insect Biochemistry and Molecular Biology, 50*, 1–17. https://doi.org/10.1016/j.ibmb.2014.03.012

Douris, V., Steinbach, D., Panteleri, R., Livadaras, I., Pickett, J. A., Van Leeuwen, T., … Vontas, J. (2016). Resistance mutation conserved between insects and mites unravels the benzoylurea insecticide mode of action on chitin biosynthesis. *Proceedings of the National Academy of Sciences of the United States of America, 113*(51), 14692–14697. https://doi.org/10.1073/pnas.1618258113

Espinosa, P. J., Contreras, J., Quinto, V., Grávalos, C., Fernández, E., & Bielza, P. (2005). Metabolic mechanisms of insecticide resistance in the western flower thrips, Frankliniella occidentalis (Pergande). *Pest Management Science, 61*(10), 1009–1015. https://doi.org/10.1002/ps.1069

Feyereisen, R., Dermauw, W., & Van Leeuwen, T. (2015). Genotype to phenotype, the molecular and physiological dimensions of resistance in arthropods. *Pesticide Biochemistry and Physiology, 121*, 61–77. https://doi.org/10.1016/j.pestbp.2015.01.004

Ffrench-Constant, R. H. (2013). The molecular genetics of insecticide resistance. *Genetics, 194*(4), 807–815. https://doi.org/10.1534/genetics.112.141895

Ffrench-Constant, R. H., Rocheleau, T. A., Steichen, J. C., & Chalmers, A. E. (1993). A point mutation in a Drosophila GABA receptor confers insecticide resistance. *Nature, 363*(6428), 449–451. https://doi.org/10.1038/363449a0

Ffrench-Constant, R. H., Pittendrigh, B., Vaughan, A., & Anthony, N. (1998). Why are there so few resistance-associated mutations in insecticide target genes? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 353*(1376), 1685–1693. https://doi.org/10.1098/rstb.1998.0319

Forcioli, D., Frey, B., & Frey, J. E. (2002). High nucleotide diversity in the para-like voltage-sensitive sodium channel gene sequence in the western flower thrips (Thysanoptera: Thripidae). *Journal of Economic Entomology, 95*(4), 838–848. https://doi.org/10.1603/0022-0493-95.4.838

Fotakis, E. A., Mastrantonio, V., Grigoraki, L., Porretta, D., Puggioli, A., Chaskopoulou, A., … Vontas, J. (2020). Identification and detection of a novel point mutation in the Chitin Synthase gene of *Culex pipiens* associated with diflubenzuron resistance. *PLoS Neglected Tropical Diseases, 14*(5), e0008284. https://doi.org/10.1371/journal.pntd.0008284

Fotoukkiaii, S. M., Wybouw, N., Kurlovs, A. H., Tsakireli, D., Pergantis, S. A., Clark, R. M., … Van Leeuwen, T. (2021). High-resolution genetic mapping reveals cis-regulatory and copy number variation in loci associated with cytochrome P450-mediated detoxification in a generalist arthropod pest. *PLOS Genetics, 17*(6), e1009422. https://doi.org/10.1371/journal.pgen.1009422

Fu, B., Li, Q., Qiu, H., Tang, L., Zeng, D., Liu, K., & Gao, Y. (2018). Resistance development, stability, cross-resistance potential, biological fitness and biochemical mechanisms of spinetoram resistance in Thrips hawaiiensis (Thysanoptera: Thripidae). *Pest Management Science, 74*(7), 1564–1574. https://doi.org/10.1002/ps.4887

Fu, B., Qiu, H., Li, Q., Tang, L., Zeng, D., Liu, K., & Gao, Y. (2019). Analysis of seasonal and annual field-evolved insecticide resistance in populations of Thrips hawaiiensis in banana orchards. *Journal of Pest Science, 92*(3), 1293–1307. https://doi.org/10.1007/s10340-019-01112-w

Gao, C.-F., Ma, S.-Z., Shan, C.-H., & Wu, S.-F. (2014). Thiamethoxam resistance selected in the western flower thrips Frankliniella occidentalis (Thysanoptera: Thripidae): Cross-resistance patterns, possible biochemical mechanisms and fitness costs analysis. *Pesticide Biochemistry and Physiology, 114*, 90–96. https://doi.org/10.1016/j.pestbp.2014.06.009

Gao, Y., Lei, Z., & Reitz, S. R. (2012). Western flower thrips resistance to insecticides: Detection, mechanisms and management strategies. *Pest Management Science, 68*(8), 1111–1121. https://doi.org/10.1002/ps.3305

Gao, Y., Kim, M. J., Kim, J. H., Jeong, I. H., Clark, J. M., & Lee, S. H. (2020). Transcriptomic identification and characterization of genes responding to sublethal doses of three different insecticides in the western flower thrips, Frankliniella occidentalis. *Pesticide Biochemistry and Physiology, 167*, 104596. https://doi.org/10.1016/j.pestbp.2020.104596

Gao, Y., Yoon, K. A., Lee, J. H., Kim, J. H., & Lee, S. H. (2022). Overexpression of glutamate-gated chloride channel in the integument is mainly responsible for emamectin benzoate resistance in the western flower thrips Frankliniella occidentalis. *Pest Management Science, 78*(10), 4140–4150. https://doi.org/10.1002/ps.7032

Gao, Y.-F., Gong, Y.-J., Cao, L.-J., Chen, J.-C., Gao, Y.-L., Mirabbalou, M., … Wei, S.-J. (2021). Geographical and interspecific variation in susceptibility of three common thrips species to the insecticide, spinetoram. *Journal of Pest Science, 94*(1), 93–99. https://doi.org/10.1007/s10340-019-01128-2

Gholami, Z., Jahromi, K. T., Hosseininaveh, V., & Mosallanejad, H. (2020). Characteristic of resistance to dichlorvos and biochemical mechanisms in the greenhouse strains of frankliniella occidentalis (Thysanoptera: Thripidae). *Journal of Crop Protection, 9*(2), 195–207.

Greenhalgh, R., Dermauw, W., Glas, J. J., Rombauts, S., Wybouw, N., Thomas, J., … Kant, M. R. (2020). Genome streamlining in a minute herbivore that manipulates its host plant. *eLife, 9*, e56689. https://doi.org/10.7554/eLife.56689

Guan, F., Zhang, J., Shen, H., Wang, X., Padovan, A., Walsh, T. K., … Wu, Y. (2021). Whole-genome sequencing to detect mutations associated with resistance to insecticides and Bt proteins in Spodoptera frugiperda. *Insect Science, 28*(3), 627–638. https://doi.org/10.1111/1744-7917.12838

Guo, L., Xie, W., Yang, Z., Xu, J., & Zhang, Y. (2020a). Genome-wide identification and expression analysis of Udp-Glucuronosyltransferases in the whitefly *Bemisia tabaci* (Gennadius) (HemipterA: Aleyrodidae). *International Journal of Molecular Sciences, 21*(22), 8492. https://doi.org/10.3390/ijms21228492

Guo, S.-K., Cao, L.-J., Song, W., Shi, P., Gao, Y.-F., Gong, Y.-J., … Wei, S.-J. (2020b). Chromosome-level assembly of the melon thrips genome yields insights into evolution of a sap-sucking lifestyle and pesticide resistance. *Molecular Ecology Resources, 20*(4), 1110–1125. https://doi.org/10.1111/1755-0998.13189

Gupta, R., Kwon, S.-Y., & Kim, S. T. (2018). An insight into the tomato spotted wilt virus (TSWV), tomato and thrips interaction. *Plant Biotechnology Reports, 12*(3), 157–163. https://doi.org/10.1007/s11816-018-0483-x

Hassan, F., Singh, K. P., Ali, V., Behera, S., Shivam, P., Das, P., & Dinesh, D. S. (2019). Detection and functional characterization of sigma class GST in Phlebotomus argentipes and its role in stress tolerance and DDT resistance. *Scientific Reports, 9*(1), 19636. https://doi.org/10.1038/s41598-019-56209-0

Hawkins, J., Mitchell, E. L., & Jones, A. K. (2022). NACHO permits functional heterologous expression of an insect homomeric α6 nicotinic acetylcholine receptor. *Pesticide Biochemistry and Physiology, 181*, 105030. https://doi.org/10.1016/j.pestbp.2021.105030

He, C., Xie, W., Yang, X., Wang, S.-L., Wu, Q.-J., & Zhang, Y.-J. (2018). Identification of glutathione S-transferases in Bemisia tabaci (Hemiptera: Aleyrodidae) and evidence that GSTd7 helps explain the difference in insecticide susceptibility between B. tabaci Middle East-Minor Asia 1 and Mediterranean. *Insect Molecular Biology, 27*(1), 22–35. https://doi.org/10.1111/imb.12337

Heckel, D. G. (2014). Insect detoxification and sequestration strategies. In C. Voelckel & G. Jander (Eds.), *Annual Plant Reviews* (pp. 77–114). John Wiley & Sons, Ltd.; https://doi.org/10.1002/9781118829783.ch3

Herron, G. A., Gunning, R. V., Cottage, E. L. A., Borzatta, V., & Gobbi, C. (2014). Spinosad resistance, esterase isoenzymes and temporal synergism in Frankliniella occidentalis (Pergande) in Australia. *Pesticide Biochemistry and Physiology, 114*, 32–37. https://doi.org/10.1016/j.pestbp.2014.07.006

Hiruta, E., Aizawa, M., Nakano, A., & Sonoda, S. (2018). Nicotinic acetylcholine receptor α6 subunit mutation (G275V) found in a spinosad-resistant strain of the flower thrips, Frankliniella intonsa (Thysanoptera: Thripidae). *Journal of Pesticide Science, 43*(4), 272–276. https://doi.org/10.1584/jpestics.D18-007

Huseth, A. S., Chappell, T. M., Langdon, K., Morsello, S. C., Martin, S., Greene, J. K., … Kennedy, G. G. (2016). *Frankliniella fusca* resistance to neonicotinoid insecticides: An emerging challenge for cotton pest management in the eastern United States. *Pest Management Science, 72*(10), 1934–1945. https://doi.org/10.1002/ps.4232

İnak, E. (2022). Geographical distribution and origin of acetylcholinesterase mutations conferring acaricide resistance in Tetranychus urticae populations from Turkey. *Experimental & Applied Acarology, 86*(1), 49–59. https://doi.org/10.1007/s10493-021-00673-9

Isman, M. B. (2019). Challenges of pest management in the twenty first century: New tools and strategies to combat old and new foes alike. *Frontiers in Agronomy, 1*, 2. https://doi.org/10.3389/fagro.2019.00002

Jacobson, A. L., Johnston, J. S., Rotenberg, D., Whitfield, A. E., Booth, W., Vargo, E. L., & Kennedy, G. G. (2013). Genome size and ploidy of Thysanoptera. *Insect Molecular Biology, 22*(1), 12–17. https://doi.org/10.1111/j.1365-2583.2012.01165.x

Jensen, S. E. (1998). Acetylcholinesterase activity associated with methiocarb resistance in a strain of western flower thrips, Frankliniella occidentalis (Pergande). *Pesticide Biochemistry and Physiology, 61*(3), 191–200. https://doi.org/10.1006/pest.1998.2359

Jones, A. K., Goven, D., Froger, J.-A., Bantz, A., & Raymond, V. (2021). The cys-loop ligand-gated ion channel gene superfamilies of the cockroaches Blattella germanica and Periplaneta americana. *Pest Management Science, 77*(8), 3787–3799. https://doi.org/10.1002/ps.6245

Jones, D. R. (2005). Plant viruses transmitted by thrips. *European Journal of Plant Pathology, 113*(2), 119–157. https://doi.org/10.1007/s10658-005-2334-1

Jouraku, A., Kuwazaki, S., Iida, H., Ohta, I., Kusano, H., Takagi, M., … Takeda, M. (2019). T929I and K1774N mutation pair and M918L single mutation identified in the voltage-gated sodium channel gene of pyrethroid-resistant Thrips tabaci (Thysanoptera: Thripidae) in Japan. *Pesticide Biochemistry and Physiology, 158*, 77–87. https://doi.org/10.1016/j.pestbp.2019.04.012

Katoh, K., Rozewicki, J., & Yamada, K. D. (2019). MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics, 20*(4), 1160–1166. https://doi.org/10.1093/bib/bbx108

Kennedy, C. J., & Tierney, K. B. (2013). Xenobiotic protection/resistance mechanisms in organisms. In E. A. Laws (Ed.), *Environmental Toxicology* (pp. 689–721). New York: Springer; https://doi.org/10.1007/978-1-4614-5764-0_23

Kim, Y. H., & Lee, S. H. (2013). Which acetylcholinesterase functions as the main catalytic enzyme in the Class Insecta? *Insect Biochemistry and Molecular Biology, 43*(1), 47–53. https://doi.org/10.1016/j.ibmb.2012.11.004

Kumm, S., & Moritz, G. (2010). Life-cycle variation, including female production by virgin females in Frankliniella occidentalis (Thysanoptera: Thripidae). *Journal of Applied Entomology, 134*(6), 491–497. https://doi.org/10.1111/j.1439-0418.2009.01473.x

Kurlovs, A. H., Snoeck, S., Kosterlitz, O., Van Leeuwen, T., & Clark, R. M. (2019). Trait mapping in diverse arthropods by bulked segregant analysis. *Current Opinion in Insect Science, 36*, 57–65. https://doi.org/10.1016/j.cois.2019.08.004

Kurlovs, A. H., De Beer, B. D., Ji, M., Vandenhole, M., De Meyer, T. D., Feyereisen, R., … Van Leeuwen, T. (2022). Trans-driven variation in expression is common among detoxification genes in the extreme generalist herbivore Tetranychus urticae. *PLOS Genetics, 18*(11), e1010333. https://doi.org/10.1371/journal.pgen.1010333

Lebedev, G., Abo-Moch, F., Gafni, G., Ben-Yakir, D., & Ghanim, M. (2013). High-level of resistance to spinosad, emamectin benzoate and carbosulfan in populations of Thrips tabaci collected in Israel. *Pest Management Science, 69*(2), 274–277. https://doi.org/10.1002/ps.3385

Lee, S. H., Clark, J. M., Ahn, Y. J., Lee, W.-J., Yoon, K. S., Kwon, D. H., & Seong, K. M. (2010). Molecular mechanisms and monitoring of permethrin resistance in human head lice. *Pesticide Biochemistry and Physiology, 97*(2), 109–114. https://doi.org/10.1016/j.pestbp.2009.04.017

Lenfant, N., Hotelier, T., Velluet, E., Bourne, Y., Marchot, P., & Chatonnet, A. (2013). ESTHER, the database of the α/β-hydrolase fold superfamily of proteins: Tools to explore diversity of functions. *Nucleic Acids Research, 41*(D1), D423–D429. https://doi.org/10.1093/nar/gks1154

Li, X., Zhu, B., Gao, X., & Liang, P. (2017). Over-expression of UDP-glycosyltransferase gene UGT2B17 is involved in chlorantraniliprole resistance in Plutella xylostella (L.). *Pest Management Science, 73*(7), 1402–1409. https://doi.org/10.1002/ps.4469

Mavridis, K., Ilias, A., Papapostolou, K. M., Varikou, K., Michaelidou, K., Tsagkarakou, A., & Vontas, J. (2022). Molecular diagnostics for monitoring insecticide resistance in the western flower thrips *Frankliniella occidentalis. Pest Management Science*, *ps.7336*. https://doi.org/10.1002/ps.7336

Meng, X., Xie, Z., Zhang, N., Ji, C., Dong, F., Qian, K., & Wang, J. (2018). Molecular cloning and characterization of GABA receptor and GluCl subunits in the western flower thrips, Frankliniella occidentalis. *Pesticide Biochemistry and Physiology, 150*, 33–39. https://doi.org/10.1016/j.pestbp.2018.06.012

Mermans, C., Dermauw, W., Geibel, S., & Van Leeuwen, T. (2017). A G326E substitution in the glutamate-gated chloride channel 3 (GluCl3) of the two-spotted spider mite Tetranychus urticae abolishes the agonistic activity of macrocyclic lactones. *Pest Management Science, 73*(12), 2413–2418. https://doi.org/10.1002/ps.4677

Minakuchi, C., Inano, Y., Shi, X., Song, D., Zhang, Y., Miura, K., … Sonoda, S. (2013). Neonicotinoid resistance and cDNA sequences of nicotinic acetylcholine receptor subunits of the western flower thrips Frankliniella occidentalis (Thysanoptera: Thripidae). *Applied Entomology and Zoology, 48*(4), 507–513. https://doi.org/10.1007/s13355-013-0212-4

Mouden, S., Sarmiento, K. F., Klinkhamer, P. G., & Leiss, K. A. (2017). Integrated pest management in western flower thrips: Past, present and future. *Pest Management Science, 73*(5), 813–822. https://doi.org/10.1002/ps.4531

Mound, L. A., & Teulon, D. A. J. (1995). Thysanoptera as Phytophagous Opportunists. In B. L. Parker, M. Skinner, & T. Lewis (Eds.), *Thrips Biology and Management* (pp. 3–19). New York: Springer; https://doi.org/10.1007/978-1-4899-1409-5_1

Mugenzi, L. M. J., Menze, B. D., Tchouakui, M., Wondji, M. J., Irving, H., Tchoupo, M., … Wondji, C. S. (2019). Cis-regulatory CYP6P9b P450 variants associated with loss of insecticide-treated bed net efficacy against Anopheles funestus. *Nature Communications, 10*(1), 4652. https://doi.org/10.1038/s41467-019-12686-5

Nault, B. A., Shelton, A. M., Gangloff-kaufmann, J. L., Clark, M. E., Werren, J. L., Cabrera-la Rosa, J. C., & Kennedy, G. G. (2006). Reproductive modes in onion thrips (Thysanoptera: Thripidae) populations from New York onion fields. *Environmental Entomology, 35*(5), 1264–1271. https://doi.org/10.1093/ee/35.5.1264

Nazemi, A., Khajehali, J., & Van Leeuwen, T. (2016). Incidence and characterization of resistance to pyrethroid and organophosphorus insecticides in Thrips tabaci (Thysanoptera: Thripidae) in onion fields in Isfahan, Iran. *Pesticide Biochemistry and Physiology, 129*, 28–35. https://doi.org/10.1016/j.pestbp.2015.10.013

Negash, B., Azerefegne, F., & Ayalew, G. (2021). Regional variation in susceptibility of thrips (Thysanoptera: Thripidae) to insecticides on onion in the Rift Valley of Ethiopia. *International Journal of Tropical Insect Science, 41*(2), 1579–1584. https://doi.org/10.1007/s42690-020-00358-7

Nguyen, D. T., Spooner-Hart, R. N., & Riegler, M. (2015). Polyploidy versus endosymbionts in obligately thelytokous thrips. *BMC Evolutionary Biology, 15*(1), 23. https://doi.org/10.1186/s12862-015-0304-6

Nguyen, V. H., Jonckheere, W., Nguyen, D. T., de Moraes, G. J., Van Leeuwen, T., & De Clercq, P. (2019). Phytoseiid mites prey effectively on thrips eggs: Evidence from predation trials and molecular analyses. *Biological Control, 137*, 104012. https://doi.org/10.1016/j.biocontrol.2019.104012

Njiru, C., Xue, W., De Rouck, S., Alba, J. M., Kant, M. R., Chruszcz, M., … Van Leeuwen, T. (2022). Intradiol ring cleavage dioxygenases from herbivorous spider mites as a new detoxification enzyme family in animals. *BMC Biology, 20*(1), 131. https://doi.org/10.1186/s12915-022-01323-1

Papapostolou, K. M., Riga, M., Samantsidis, G.-R., Skoufa, E., Balabanidou, V., Van Leeuwen, T., & Vontas, J. (2022). Over-expression in cis of the midgut P450 CYP392A16 contributes to abamectin resistance in Tetranychus urticae. *Insect Biochemistry and Molecular Biology, 142*, 103709. https://doi.org/10.1016/j.ibmb.2021.103709

Pavlidi, N., Vontas, J., & Van Leeuwen, T. (2018). The role of glutathione S-transferases (GSTs) in insecticide resistance in crop pests and disease vectors. *Current Opinion in Insect Science, 27*, 97–102. https://doi.org/10.1016/j.cois.2018.04.007

Pittendrigh, B. R., Margam, V. M., Walters, K. R., Jr., Steele, L. D., Olds, B. P., Sun, L., … Clark, J. M. (2014). Understanding resistance and induced responses of insects to xenobiotics and insecticides in the age of "omics" and systems biology. In D. W. Onstad (Ed.), *Insect Resistance Management* (pp. 55–98). Academic Press. https://doi.org/10.1016/B978-0-12-396955-2.00003-5

Puinean, A. M., Lansdell, S. J., Collins, T., Bielza, P., & Millar, N. S. (2013). A nicotinic acetylcholine receptor transmembrane point mutation (G275E) associated with resistance to spinosad in Frankliniella occidentalis. *Journal of Neurochemistry, 124*(5), 590–601. https://doi.org/10.1111/jnc.12029

Qi, W., Ma, X., He, W., Chen, W., Zou, M., Gurr, G. M., … You, M. (2016). Characterization and expression profiling of ATP-binding cassette transporter genes in the diamondback moth, Plutella xylostella (L.). *BMC Genomics, 17*(1), 760. https://doi.org/10.1186/s12864-016-3096-1

R4P Network (2016). Trends and challenges in pesticide resistance detection. *Trends in Plant Science, 21*(10), 834–853. https://doi.org/10.1016/j.tplants.2016.06.006

Rane, R. V., Walsh, T. K., Pearce, S. L., Jermiin, L. S., Gordon, K. H., Richards, S., & Oakeshott, J. G. (2016). Are feeding preferences and insecticide resistance associated with the size of detoxifying enzyme families in insect herbivores? *Current Opinion in Insect Science, 13*, 70–76. https://doi.org/10.1016/j.cois.2015.12.001

Rane, R. V., Ghodke, A. B., Hoffmann, A. A., Edwards, O. R., Walsh, T. K., & Oakeshott, J. G. (2019). Detoxifying enzyme complements and host use phenotypes in 160 insect species. *Current Opinion in Insect Science, 31*, 131–138. https://doi.org/10.1016/j.cois.2018.12.008

Reitz, S. R., Gao, Y., Kirk, W. D. J., Hoddle, M. S., Leiss, K. A., & Funderburk, J. E. (2020). Invasion biology, ecology, and management of western flower thrips. *Annual Review of Entomology, 65*(1), 17–37. https://doi.org/10.1146/annurev-ento-011019-024947

Riga, M., Bajda, S., Themistokleous, C., Papadaki, S., Palzewicz, M., Dermauw, W., … Van Leeuwen, T. (2017). The relative contribution of target-site mutations in complex acaricide resistant phenotypes as assessed by marker assisted backcrossing in Tetranychus urticae. *Scientific Reports, 7*(1), 9202. https://doi.org/10.1038/s41598-017-09054-y

Rinkevich, F. D., Du, Y., & Dong, K. (2013). Diversity and convergence of sodium channel mutations involved in resistance to pyrethroids. *Pesticide Biochemistry and Physiology, 106*(3), 93–100. https://doi.org/10.1016/j.pestbp.2013.02.007

Rosen, R., Lebedev, G., Kontsedalov, S., Ben-Yakir, D., & Ghanim, M. (2021). A de novo transcriptomics approach reveals genes involved in Thrips tabaci resistance to spinosad. *Insects, 12*(1), 67. https://doi.org/10.3390/insects12010067

Rotenberg, D., Baumann, A. A., Ben-Mahmoud, S., Christiaens, O., Dermauw, W., Ioannidis, P., … Richards, S. (2020). Genome-enabled insights into the biology of thrips as crop pests. *BMC Biology, 18*(1), 142. https://doi.org/10.1186/s12915-020-00862-9

Rufener, L., Kaur, K., Sarr, A., Aaen, S. M., & Horsberg, T. E. (2020). Nicotinic acetylcholine receptors: Ex-vivo expression of functional, non-hybrid, heteropentameric receptors from a marine arthropod, Lepeophtheirus salmonis. *PLoS Pathogens, 16*(7), e1008715. https://doi.org/10.1371/journal.ppat.1008715

Sheng, C.-W., Jia, Z.-Q., Ozoe, Y., Huang, Q.-T., Han, Z.-J., & Zhao, C.-Q. (2018). Molecular cloning, spatiotemporal and functional expression of GABA receptor subunits RDL1 and RDL2 of the rice stem borer Chilo suppressalis. *Insect Biochemistry and Molecular Biology, 94*, 18–27. https://doi.org/10.1016/j.ibmb.2018.01.003

Shi, P., Guo, S.-K., Gao, Y.-F., Chen, J.-C., Gong, Y.-J., Tang, M.-Q., … Wei, S.-J. (2021). Association between susceptibility of *Thrips palmi* to spinetoram and frequency of G275E mutation provides basis for molecular quantification of field-evolved resistance. *Journal of Economic Entomology, 114*(1), 339–347. https://doi.org/10.1093/jee/toaa314

Shi, T., Tang, P., Wang, X., Yang, Y., & Wu, Y. (2022). CRISPR-mediated knockout of nicotinic acetylcholine receptor (nAChR) α6 subunit confers high levels of resistance to spinosyns in Spodoptera frugiperda. *Pesticide Biochemistry and Physiology, 187*, 105191. https://doi.org/10.1016/j.pestbp.2022.105191

Silva, W. M., Berger, M., Bass, C., Williamson, M., Moura, D. M. N., Ribeiro, L. M. S., & Siqueira, H. A. A. (2016). Mutation (G275E) of the nicotinic acetylcholine receptor α6 subunit is associated with high levels of resistance to spinosyns in Tuta absoluta (Meyrick) (Lepidoptera: Gelechiidae). *Pesticide Biochemistry and Physiology, 131*, 1–8. https://doi.org/10.1016/j.pestbp.2016.02.006

Simma, E. A., Hailu, B., Jonckheere, W., Rogiers, C., Duchateau, L., Dermauw, W., & Van Leeuwen, T. (2020). Acaricide resistance status and identification of resistance mutations in populations of the two-spotted spider mite Tetranychus urticae from Ethiopia. *Experimental & Applied Acarology, 82*(4), 475–491. https://doi.org/10.1007/s10493-020-00567-2

Singh, O. P., Dykes, C. L., Das, M. K., Pradhan, S., Bhatt, R. M., Agrawal, O. P., & Adak, T. (2010). Presence of two alternative kdr-like mutations, L1014F and L1014S, and a novel mutation, V1010L, in the voltage gated Na+ channel of Anopheles culicifacies from Orissa, India. *Malaria Journal, 9*(1), 146. https://doi.org/10.1186/1475-2875-9-146

Snoeck, S., Greenhalgh, R., Tirry, L., Clark, R. M., Van Leeuwen, T., & Dermauw, W. (2017). The effect of insecticide synergist treatment on genome-wide gene expression in a polyphagous pest. *Scientific Reports, 7*(1), 13440. https://doi.org/10.1038/s41598-017-13397-x

Snoeck, S., Wybouw, N., Van Leeuwen, T., & Dermauw, W. (2018). Transcriptomic plasticity in the arthropod generalist *Tetranychus urticae* upon long-term acclimation to different host plants. *G3 Genes|Genomes|Genetics, 8*(12), 3865–3879. https://doi.org/10.1534/g3.118.200585

Sparks, T. C., Dripps, J. E., Watson, G. B., & Paroonagian, D. (2012). Resistance and cross-resistance to the spinosyns – a review and analysis. *Pesticide Biochemistry and Physiology, 102*(1), 1–10. https://doi.org/10.1016/j.pestbp.2011.11.004

Sun, L.-N., Shen, X.-J., Cao, L.-J., Chen, J.-C., Ma, L.-J., Wu, S.-A., … Wei, S.-J. (2022). Increasing frequency of G275E mutation in the nicotinic acetylcholine receptor α6 subunit conferring spinetoram resistance in invading populations of western flower thrips in China. *Insects, 13*(4), 331. https://doi.org/10.3390/insects13040331

Suzuki, Y., Shiotsuki, T., Jouraku, A., Miura, K., & Minakuchi, C. (2017). Benzoylurea resistance in western flower thrips Frankliniella occidentalis (Thysanoptera: Thripidae): the presence of a point mutation in chitin synthase 1. *Journal of Pesticide Science, 42*(3), 93–96. https://doi.org/10.1584/jpestics.D17-023

Tadatsu, M., Sakashita, R., Panteleri, R., Douris, V., Vontas, J., Shimotsuma, Y., … Osakabe, M. (2022). A mutation in chitin synthase I associated with etoxazole resistance in the citrus red mite *Panonychus citri* (Acari: Tetranychidae) and its uneven geographical distribution in Japan. *Pest Management Science, 78*(10), 4028–4036. https://doi.org/10.1002/ps.7021

Thalavaisundaram, S., Wilkes, M. A., Mansfield, S., Rose, H. A., & Herron, G. A. (2012). Esterases and glutathione S-transferases contribute to pyrethroid resistance in western flower thrips, Frankliniella occidentalis. *Australian Journal of Entomology, 51*(4), 272–278. https://doi.org/10.1111/j.1440-6055.2012.00865.x

Toda, S., & Morishita, M. (2009). Identification of three point mutations on the sodium channel gene in pyrethroid-resistant Thrips tabaci (Thysanoptera: Thripidae). *Journal of Economic Entomology, 102*(6), 2296–2300. https://doi.org/10.1603/029.102.0635

Trifinopoulos, J., Nguyen, L.-T., von Haeseler, A., & Minh, B. Q. (2016). W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research, 44*(W1), W232–W235. https://doi.org/10.1093/nar/gkw256

Van Leeuwen, T., & Dermauw, W. (2016). The molecular evolution of xenobiotic metabolism and resistance in chelicerate mites. *Annual Review of Entomology, 61*(1), 475–498. https://doi.org/10.1146/annurev-ento-010715-023907

Van Leeuwen, T., Demaeght, P., Osborne, E. J., Dermauw, W., Gohlke, S., Nauen, R., … Clark, R. M. (2012). Population bulk segregant mapping uncovers resistance mutations and the mode of action of a chitin synthesis inhibitor in arthropods. *Proceedings of the National Academy of Sciences of the United States of America, 109*(12), 4407–4412. https://doi.org/10.1073/pnas.1200068109

Van Leeuwen, T., Dermauw, W., Mavridis, K., & Vontas, J. (2020). Significance and interpretation of molecular diagnostics for insecticide resistance management of agricultural pests. *Current Opinion in Insect Science, 39*, 69–76. https://doi.org/10.1016/j.cois.2020.03.006

van Lenteren, J. C., Bolckmans, K., Köhl, J., Ravensberg, W. J., & Urbaneja, A. (2018). Biological control using invertebrates and microorganisms: Plenty of new opportunities. *BioControl, 63*(1), 39–59. https://doi.org/10.1007/s10526-017-9801-4

Villatte, F., Marcel, V., Estrada-Mondaca, S., & Fournier, D. (1998). Engineering sensitive acetylcholinesterase for detection of organophosphate and carbamate insecticides. *Biosensors & Bioelectronics, 13*(2), 157–164. https://doi.org/10.1016/S0956-5663(97)00108-5

Vontas, J. G., Hejazi, M. J., Hawkes, N. J., Cosmidis, N., Loukas, M., & Hemingway, J. (2002). Resistance-associated point mutations of organophosphate insensitive acetylcholinesterase, in the olive fruit fly Bactrocera oleae. *Insect Molecular Biology, 11*(4), 329–336. https://doi.org/10.1046/j.1365-2583.2002.00343.x

Wan, Y., Yuan, G., He, B., Xu, B., Xie, W., Wang, S., … Zhou, X. (2018). Foccα6, a truncated nAChR subunit, positively correlates with spinosad resistance in the western flower thrips, Frankliniella occidentalis (Pergande). *Insect Biochemistry and Molecular Biology, 99*, 1–10. https://doi.org/10.1016/j.ibmb.2018.05.002

Wang, J., Ma, H., Zuo, Y., Yang, Y., & Wu, Y. (2020a). CRISPR-mediated gene knockout reveals nicotinic acetylcholine receptor (nAChR) subunit α6 as a target of spinosyns in Helicoverpa armigera. *Pest Management Science, 76*(9), 2925–2931. https://doi.org/10.1002/ps.5889

Wang, R., Wang, Z., Luo, C., & Yang, G. (2020b). Characterization of pyridalyl resistance in a laboratory-selected strain of Frankliniella occidentalis. *Pesticide Biochemistry and Physiology, 166*, 104564. https://doi.org/10.1016/j.pestbp.2020.104564

Wang, S.-Y., Zhou, X.-H., Zhang, A.-S., Li, L.-L., Men, X.-Y., Zhang, S.-C., … Yu, Y. (2012). Resistance mechanisms and cross-resistance of phoxim-resistant Frankliniella occidentalis Pergande population. *Ying Yong Sheng Tai Xue Bao, 23*(7), 1933–1939.

Wang, X., Puinean, A. M., O'Reilly, A. O., Williamson, M. S., Smelt, C. L. C., Millar, N. S., & Wu, Y. (2017). Mutations on M3 helix of Plutella xylostella glutamate-gated chloride channel confer unequal resistance to abamectin by two different mechanisms. *Insect Biochemistry and Molecular Biology, 86*, 50–57. https://doi.org/10.1016/j.ibmb.2017.05.006

Wang, Z., Mound, L., & Tong, X. (2019). Frankliniella species from China, with nomenclatural changes and illustrated key (Thysanoptera, Thripidae). *ZooKeys, 873*, 43–53. https://doi.org/10.3897/zookeys.873.36863

Wang, Z.-H., Gong, Y.-J., Jin, G.-H., Li, B.-Y., Chen, J.-C., Kang, Z.-J., … Wei, S.-J. (2016). Field-evolved resistance to insecticides in the invasive western flower thrips Frankliniella occidentalis (Pergande) (Thysanoptera: Thripidae) in China. *Pest Management Science, 72*(7), 1440–1444. https://doi.org/10.1002/ps.4200

Weedall, G. D., Mugenzi, L. M. J., Menze, B. D., Tchouakui, M., Ibrahim, S. S., Amvongo-Adjia, N., … Wondji, C. S. (2019). A cytochrome P450 allele confers pyrethroid resistance on a major African malaria vector, reducing insecticide-treated bednet efficacy. *Science Translational Medicine, 11*(484), eaat7386. https://doi.org/10.1126/scitranslmed.aat7386

Weill, M., Berthomieu, A., Berticat, C., Lutfalla, G., Nègre, V., Pasteur, N., … Raymond, M. (2004a). Insecticide resistance: A silent base prediction. *Current Biology, 14*(14), R552–R553. https://doi.org/10.1016/j.cub.2004.07.008

Weill, M., Malcolm, C., Chandre, F., Mogensen, K., Berthomieu, A., Marquine, M., & Raymond, M. (2004b). The unique mutation in ace-1 giving high insecticide resistance is easily detectable in mosquito vectors. *Insect Molecular Biology, 13*(1), 1–7. https://doi.org/10.1111/j.1365-2583.2004.00452.x

Wolstenholme, A. J. (2012). Glutamate-gated chloride channels. *The Journal of Biological Chemistry, 287*(48), 40232–40238. https://doi.org/10.1074/jbc.R112.406280

Wondji, C. S., Dabire, R. K., Tukur, Z., Irving, H., Djouaka, R., & Morgan, J. C. (2011). Identification and distribution of a GABA receptor mutation conferring dieldrin resistance in the malaria vector Anopheles funestus in Africa. *Insect Biochemistry and Molecular Biology, 41*(7), 484–491. https://doi.org/10.1016/j.ibmb.2011.03.012

Wu, M., Gotoh, H., Waters, T., Walsh, D. B., & Lavine, L. C. (2014). Identification of an alternative knockdown resistance (kdr)-like mutation, M918L, and a novel mutation, V1010A, in the Thrips tabaci voltage-gated sodium channel gene. *Pest Management Science, 70*(6), 977–981. https://doi.org/10.1002/ps.3638

Wybouw, N., Kosterlitz, O., Kurlovs, A. H., Bajda, S., Greenhalgh, R., Snoeck, S., … Clark, R. M. (2019). Long-term population studies uncover the genome structure and genetic basis of xenobiotic and host plant adaptation in the herbivore Tetranychus urticae. *Genetics, 211*(4), 1409–1427. https://doi.org/10.1534/genetics.118.301803

Xie, W., Yang, X., Chen, C., Yang, Z., Guo, L., Wang, D., … Zhang, Y. (2018). The invasive MED/Q Bemisia tabaci genome: A tale of gene loss and gene gain. *BMC Genomics, 19*(1), 68. https://doi.org/10.1186/s12864-018-4448-9

Xue, W., Mermans, C., Papapostolou, K.-M., Lamprousi, M., Christou, I.-K., Inak, E., … Van Leeuwen, T. (2021). Untangling a Gordian knot: The role of a GluCl3 I321T mutation in abamectin resistance in Tetranychus urticae. *Pest Management Science, 77*(4), 1581–1593. https://doi.org/10.1002/ps.6215

Yokoyama, T., Kashima, T., & Toda, S. (2014). Point mutations of the sodium channel gene associated with the Fenpropathrin resistance in Scirtothrips dorsalis and discrimination of resistant individuals using the PCR-RFLP assay. *Japanese Journal of Applied Entomology and Zoology, 58*(1), 59–62. https://doi.org/10.1303/jjaez.2014.59

Yue, W.-B., Zhi, J.-R., Liu, L., Hou, X.-L., & Ye, M. (2022). The responses of detoxification enzyme and gene expression in western flower thrips, Frankliniella occidentalis, to new challenging hosts. *Arthropod-Plant Interactions, 16*(1), 63–76. https://doi.org/10.1007/s11829-022-09884-2

Zeng, B., Chen, F.-R., Liu, Y.-T., Guo, D., Zhang, Y.-J., Feng, Z.-R., … Gao, C.-F. (2022). A chitin synthase mutation confers widespread resistance to buprofezin, a chitin synthesis inhibitor, in the brown planthopper, Nilaparvata lugens. *Journal of Pest Science*. https://doi.org/10.1007/s10340-022-01538-9

Zhang, K., Yuan, J., Wang, J., Hua, D., Zheng, X., Tao, M., … Wu, Q. (2022a). Susceptibility levels of field populations of Frankliniella occidentalis (Thysanoptera: Thripidae) to seven insecticides in China. *Crop Protection (Guildford, Surrey), 153*, 105886. https://doi.org/10.1016/j.cropro.2021.105886

Zhang, Y., Yang, B., Yu, N., Luo, G., Gao, H., Lin, X., & Liu, Z. (2022b). Insecticide resistance associated overexpression of two sigma GST genes assists Nilaparvata lugens to remedy oxidative stress from feeding on resistant rice variety. *Pesticide Biochemistry and Physiology, 188*, 105230. https://doi.org/10.1016/j.pestbp.2022.105230

Zhao, G. Y., Liu, W., & Knowles, C. O. (1994). Mechanisms associated with diazinon resistance in western flower thrips. *Pesticide Biochemistry and Physiology, 49*(1), 13–23. https://doi.org/10.1006/pest.1994.1030

Zimmer, C. T., Garrood, W. T., Puinean, A. M., Eckel-Zimmer, M., Williamson, M. S., Davies, T. G. E., & Bass, C. (2016). A CRISPR/Cas9 mediated point mutation in the alpha 6 subunit of the nicotinic acetylcholine receptor confers resistance to spinosad in Drosophila melanogaster. *Insect Biochemistry and Molecular Biology, 73*, 62–69. https://doi.org/10.1016/j.ibmb.2016.04.007

Zuo, Y., Xue, Y., Lu, W., Ma, H., Chen, M., Wu, Y., … Hu, Z. (2020). Functional validation of nicotinic acetylcholine receptor (nAChR) α6 as a target of spinosyns in Spodoptera exigua utilizing the CRISPR/Cas9 system. *Pest Management Science, 76*(7), 2415–2422. https://doi.org/10.1002/ps.5782

Zuo, Y.-Y., Xue, Y.-X., Wang, Z.-Y., Ren, X., Aioub, A. A. A., Wu, Y.-D., … Hu, Z.-N. (2022). Knockin of the G275E mutation of the nicotinic acetylcholine receptor (nAChR) α6 confers high levels of resistance to spinosyns in Spodoptera exigua. *Insect Science, 29*(2), 478–486. https://doi.org/10.1111/1744-7917.12922

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