Western Flower Thrips (Thysanoptera: Thripidae) and Insecticide Resistance: An Overview and Strategies to Mitigate Insecticide Resistance Development[1]

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Abstract Western flower thrips, *Frankliniella occidentalis* (Pergande), are one of the most-destructive insect pests of greenhouse-grown horticultural crops worldwide due to the direct and indirect damage they cause to plants. Western flower thrips induce direct damage by feeding on leaves and flowers and also cause indirect damage by vectoring certain tospoviruses including *Impatiens necrotic spot* and *Tomato spotted wilt* viruses. As a result, the threshold for this insect pest is near zero. Consequently, the primary means of suppressing populations of western flower thrips in greenhouse production systems is the application of insecticides. In general, insecticides are inexpensive, easy to apply, and relatively effective. However, the selection pressure placed on western flower thrips populations due to intensive applications of insecticides has resulted in severe problems associated with the development of resistance. Therefore, in order to avoid the prospect of insecticide resistance developing in western flower thrip populations, greenhouse producers must implement a multitude of plant protection strategies including scouting, insecticide rotations, insecticide mixtures, and the use of alternative insecticides (e.g., entomopathogenic fungi and insect growth regulators) with broad-spectrum modes of action.

Key Words resistance, selection pressure, plant protection, insecticides

Western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), are one of the most-destructive insect pests of greenhouse-grown horticultural crops, including vegetables and ornamentals (Helyer and Brobyn 1992, Jensen 2000a, Kirk and Terry 2003, Lewis 1997,). Direct plant damage associated with western flower thrips is a consequence of their feeding. Western flower thrips possess piercing-sucking mouthparts that are used to obtain nutrients from plant cells (Harrewijn et al. 1996), which can result in cell death and leaf or flower deformation and can negatively impact marketability due to a decreased aesthetic value (Childers 1997, Chisholm and Lewis 1984, Jensen 2000a). Indirect damage is affiliated with adult transmission of the tospoviruses, *Impatiens necrotic spot* or *Tomato spotted wilt* virus, which reduce crop aesthetic values and marketability (Allen and Broadbent 1986, Pappu et al. 2009, Wijkamp et al. 1995). Therefore, due to direct and indirect damage, greenhouse producers have minimal tolerance for

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this insect pest. Consequently, insecticides are the primary means of suppressing western flower thrips populations in order to mitigate any direct and/or indirect damage (Allen et al. 1993, Cloyd 2009a, Gao et al. 2012, Parrella 1995, Parrella and Murphy 1996). Insecticides, however, may be ineffective in dealing with western flower thrips populations because eggs are inserted into leaf tissues, and pupae are typically located in the growing medium, which protects these life stages from exposure to insecticides (Mound 1996, Reitz 2009). The natural behavior of western flower thrips, where individuals reside in concealed, enclosed areas on plants such as unopened terminal or flower buds, may reduce or limit direct exposure to spray applications of contact insecticides (Hansen et al. 2003, Jensen 2000a, Zhang et al. 2008). In addition, and most importantly, western flower thrips populations have developed resistance to many insecticides (Broadbent and Pree 1997, Gao et al. 2012, Helyer and Brobyn 1992, Immaraju et al. 1992,). Therefore, this paper will focus on two topics related to the use of insecticides against western flower thrips: (a) insecticide resistance and (b) strategies that may mitigate insecticide resistance developing in western flower thrips populations.

Insecticide Resistance

Western flower thrips feed on a range of greenhouse-grown horticultural crops, which increases their exposure to insecticide applications, even insecticides targeting other insect or mite pests. As a result, western flower thrips have a high propensity for developing resistance to different insecticides (Jensen 2000a). The intense selection pressure placed on western flower thrips populations due to frequent applications of insecticides exacerbates the potential for resistance to develop. In addition, natural populations of western flower thrips may already possess resistant alleles at low frequencies before exposure to insecticides. The possession of pre-existing resistant traits increases the likelihood for resistance to develop in western flower thrips populations (Roush and McKenzie 1987). Furthermore, multiple generations per year in greenhouses increases the possibility of western flower thrips populations developing resistance to insecticides (Immaraju et al. 1992). The intensive use of insecticides removes susceptible individuals from the population, consequently increasing the proportion or frequency of individuals with resistant genotypes (Gao et al. 2012). Therefore, excessive use of insecticides will induce rapid development of resistance due to selection pressure for resistant individuals (ffrench-Constant and Roush 1990).

The first case of western flower thrips resistance to insecticides was reported in 1961 when the chlorinated cyclodiene, toxaphene, was found to be ineffective in suppressing populations of the western flower thrips (Race 1961). Although there have been subsequent instances of reduced efficacy of insecticides against western flower thrips, the first actual record affiliated with resistance occurred almost 30 years later (Robb 1989). Worldwide there are currently 153 documented cases associated with western flower thrips populations that are resistant to insecticides in at least seven chemical classes (Arthropod Pesticide Resistance Database, Michigan State University, East Lansing, MI, http://www.pesticideresitance.org; accessed November 2015). Furthermore, differences in resistance may occur between the "lupin" and "greenhouse" strains of western flower thrips (Martin and Workman 1994). Western flower thrips populations are continually exposed to pesticide applications intended to target other pests such as aphids, whiteflies, and mites affiliated with multiple-pest complexes (Hussey 1965, Diabate et al. 2002), thus increasing the rate of resistance development to specific pesticides (Reitz et al. 2003). Another concern is that label rates of pesticides (insecticides and miticides) often vary depending on the specific pest; therefore, a label rate for western flower thrips may be lower or higher than that for other pests, which could possibly enhance the development of resistance due to increased exposure to different pesticides.

There is a well-substantiated hypothesis that only using insecticides to deal with western flower thrips populations in greenhouse production systems will eventually lead to populations developing resistance (Georghiou 1986). The rate of resistance development in western flower thrips populations is primarily associated with three biological parameters: (a) rapid (short) generation time, (b) high female reproductive capacity (fecundity), and (c) a haplo-diploid breeding system (Bielza et al. 2008, Brodsgaard 1989, Denholm et al. 1998, Hou et al. 2014, Jensen 1998, 2000a, Reitz 2009). The rapid generation time allows for multiple generations to be present simultaneously during a crop production cycle (Gaum et al. 1994, Gerin et al. 1994), with generations overlapping continuously. As a result, females can mate with resistant progeny (off-spring) that subsequently increases the frequency of resistant alleles in a population (Immaraju et al. 1992). Individuals that survive exposure to an insecticide may pass on resistant traits to the next generation, thus enriching the gene pool with resistant genes (Jensen 2000a). A high female reproductive capacity or fecundity means that females lay between 150 and 300 eggs during their 45-day lifespan (Gerin et al. 1999), which potentially increases the number of individuals in subsequent generations that are exposed to insecticides.

A haplo-diploid breeding system involves resistant genes in males (haploid with one set of chromosomes) that are directly exposed to selection after an insecticide application, which accelerates the rate of resistance development. Certain genes/alleles associated with resistance are fully expressed in haploid males whereas completely diploid (double set of chromosomes) individuals may only possess resistance if affiliated with recessive or codominant traits (Carrière 2003, Denholm et al. 1998). Therefore, selection for resistance is enhanced in haploid individuals as compared to diploid individuals.

The extensive movement of plant material, both regionally and internationally, has increased problems with western flower thrips populations (Brodsgaard 1994). Moreover, the development of insecticide resistance is an international issue, as resistant genes/alleles associated with western flower thrips populations can be spread through international trade of plant material from off-shore facilities that utilize insecticides against western flower thrips, which, in some cases, are not registered for use in the United States (R.A.C. pers. obs.). Furthermore, the international trade of moving plant material from one country to another may indiscriminately spread western flower thrips populations. In addition, the international trade of plant material may indirectly spread populations (or variants) of western flower thrips with resistant genes/alleles or specific resistance mechanisms (Denholm and Jespersen 1998), which could consequently exacerbate the problem of insecticide resistance (Jensen 2000a). Therefore, mitigating western flower thrips resistance must be dealt with on a global scale involving collaborations among countries (Zhang et al. 2008), which may dictate the need to monitor for and possibly restrict the movement of plant material infested with western flower thrips. Moreover, it will be necessary to obtain records of insecticides used 2 weeks prior to shipping so that greenhouse producers can avoid using similar insecticides once plants are incorporated into production systems. Although the Animal and Plant Health Inspection Service already deals with screening international imports of insects and plants, the problem is that when plant material is received, inspections only account for approximately 10% of all imports due to labor demand and the large quantity of imports. Furthermore, in some countries, phytosanitary regulations are completely absent (Herrick pers. comm.).

One hypothesis is that the absence of susceptible individuals immigrating into western flower thrips populations enhances resistance development (Bielza et al. 2008). However, the presumption is that individuals of wild, field populations of western flower thrips immigrating into greenhouses are actually susceptible (no insecticide resistance) and will breed with resistant individuals, thus delaying resistance by diluting the gene pool of resistant individuals (Georghiou and Taylor 1977). In addition, breeding with resistant individuals will reduce the frequency of resistant alleles in the population (Jensen 2000a) which assumes, however, that the population of individuals immigrating is in fact not resistant to insecticides. Nevertheless, many insecticides used in greenhouse production facilities are initially introduced for use in agricultural cropping systems (R.A.C. pers. obs.). Therefore, immigrating individuals may, in fact, possess resistant alleles or they may not (Jensen 2000a). Moreover, immigration of resistant individuals exposed to insecticides used in agricultural cropping systems may increase the rate at which resistance develops to insecticides registered for use in greenhouses (Immaraju et al. 1992).

Insecticide resistance is prevalent in many western flower thrips populations worldwide and, as noted above, the extensive use of insecticides over the years has led to certain western flower thrips populations developing resistance to insecticides in seven chemical classes including organophosphate (e.g., diazinon and acephate) (Brodsgaard 1994, Zhao et al. 1994), carbamate (e.g., bendiocarb, methiocarb, and methomyl) (Jensen 1998, Zhao et al. 1995a), pyrethroid (e.g., fenvalerate, cypermethrin, and bifenthrin) (Herron and Gullick 2001, Zhao et al. 1995b), neonicotinoid (e.g., imidacloprid) (Herron and James 2005, Zhao et al. 1995c), spinosyn (e.g., spinosad) (Herron and James 2005, Loughner et al. 2005), macrocycle lactone (e.g., abamectin) (Immaraju et al. 1992, Kontsedalov et al. 1998), and pyrazole (e.g., fipronil) (Herron and James 2005). The means by which western flower thrips populations develop resistance is associated with certain resistance mechanisms.

The resistance mechanisms affiliated with western flower thrips populations include enhanced metabolic detoxification and target site modifications (Brodsgaard 1994, Espinosa et al. 2005, Herron and James 2005, Jensen 2000a, Zhao et al. 1995b). In regard to metabolic detoxification, there are three primary enzyme systems involved including esterases, glutathione *S*-transferases, and cytochrome *P*-450 mono-oxygenases (Maymo et al. 2002, Soderland and Bloomquist 1990). The main function of these enzyme systems is to convert hydrophobic (water-hating) compounds, such as insecticides, into less-biologically active compounds that are hydrophilic (water-loving) and are subsequently removed during excretion

(Jensen 2000a). In addition to enhanced metabolic detoxification, insensitive acetylcholinesterase has been implicated as a resistance mechanism to organophosphates (Zhao et al. 1994). Furthermore, multiple resistance mechanisms may be involved or coexist in a single strain or population of western flower thrips (Jensen 1998, 2000a).

Because western flower thrips are highly polyphagous, feeding on a multitude of horticultural and ornamental plant types, populations of western flower thrips may have inherently evolved the genes/alleles that encode for the three enzyme systems mentioned above, thus promoting resistance development (Li et al. 2007). The most-important metabolic resistance enzyme system affiliated with western flower thrips populations is the cytochrome *P*-450 mono-oxygenases that confer cross-resistance (based on a single mechanism conferring resistance to insecticides in the same chemical class and/or having similar modes of action) to insecticides within and among different chemical classes (Espinosa et al. 2005). However, cross-resistance depends on the insecticide chemical class, as reports have indicated that 'knockdown resistance' may be responsible for pyrethroid resistance in certain greenhouse populations of western flower thrips (Immaraju et al. 1992, Zhao et al. 1995b). Moreover, modifications to the enzyme, acetylcholinesterase, may be responsible for resistance to insecticides in the chemical classes associated with organophosphates (e.g., diazinon) and carbamates (e.g., methiocarb) (Jensen 2000b, Zhao et al. 1994). Nonetheless, other mechanisms, such as glutathione *S*-transferases, esterases, target-site sensitivity, altered acetylcholinesterace, and even reduced penetration, may be involved in resistance to different insecticides (Espinosa et al. 2005).

Spinosad (Conserve®, Dow AgroSciences LLC; Indianapolis, IN), which is one of the most-widely used insecticides to suppress western flower thrips populations in greenhouse production systems (Loughner et al. 2005), became less effective as a consequence of resistance developing in western flower thrips populations, primarily due to overuse by greenhouse producers (Bielza et al. 2007, Loughner et al. 2005). For instance, failures in suppressing western flower thrips populations with spinosad, which occurred in Florida in 2006, were associated with resistance (Weiss et al. 2009). However, the mechanism involved is not metabolic detoxification but appears to be related to modifications, alterations, or reduced sensitivity of the target site (e.g., nicotinic acetylcholine receptor) (Bielza et al. 2007, Gao et al. 2012, Zhang et al. 2008) and may also be subsequently influenced by several genes or alleles (Zhang et al. 2008). In fact, spinosad resistance may be monogenic (when only one gene confers resistance, resulting in rapid development of resistance) or polygenic (when more than one gene confers resistance, leading to slow resistance development) (Bielza et al. 2007, Zhang et al. 2008). Furthermore, Hou et al. (2014) reported that resistance to spinosad was completely recessive and autosomal.

A major problem is dealing with western flower thrips populations having multiple resistance mechanisms to certain insecticides, which increases the probability of cross-resistance to unrelated insecticides (Gao et al. 2012). For instance, western flower thrips populations may possess two different resistance mechanisms, such as increased acetylcholinesterase activity and insensitive acetylcholinesterase (Jensen 1998, Zhao et al. 1994). There is the perceived implication that the level (based on fitness and stability) of resistance within a western flower thrips population will diminish more rapidly in the absence of insecticide exposure. Resistance, in general, has been observed to be affiliated with fitness costs (Roush and Daly 1990) including reduced longevity, fecundity, fertility, or decreased development time (Argentine et al. 1989, Ferrari and Georghiou 1981). However, western flower thrips populations may not exhibit any fitness costs in regard to insecticide resistance (Bielza et al. 2008). Consequently, a lack of fitness costs enhances the stability of resistance, thereby reducing the prospects of reverting populations back to susceptibility (Roush 1993), which may accelerate the rate of resistance development. Furthermore, the speed or rate of resistance development may be associated with resistant females having a higher fecundity and fertility than susceptible females (Bielza et al. 2008).

Another factor related to insecticide resistance in western flower thrips populations is demographics. The effect of demographics (e.g., north versus south) can influence the selection pressure placed on western flower thrips populations due to differences in longevity of the growing season and, consequently, the number and frequency of insecticide applications, which can influence the propensity for resistance to develop. Moreover, plant material that contains western flower thrips populations that were previously exposed to insecticides may be moved northward (R.A.C. pers. obs.). Typically, during early spring through late fall, greenhouse producers may conduct two to three applications every 5 to 7 days to suppress western flower thrips populations (Robb and Parrella 1995). Any subsequent applications are conducted to kill larvae and adults that were in the egg or pupal stages during previous applications (Parrella 1995).

Strategies that May Mitigate Insecticide Resistance

There needs to be a realization that greenhouse producers are going to continue to use insecticides against western flower thrips due to low tolerance for this insect pest. However, alternative plant protection strategies need to be implemented including cultural control (e.g., fertility), sanitation (e.g., weed and plant debris removal), physical control (e.g., screening greenhouse openings), and biological control (e.g., releasing predatory mites). These strategies, which are well known, may help reduce the selection pressure placed on western flower thrips populations from insecticide applications (Cloyd 2009a, 2015). There are a number of strategies that greenhouse producers currently use and can implement in the future to avoid the prospect of insecticide resistance developing in western flower thrips populations. These include scouting, insecticide rotations, insecticide mixtures, and the use of alternative insecticides with broad-spectrum modes of action.

Scouting. In general, scouting involves routinely monitoring western flower thrips populations using colored sticky cards (Cloyd and Sadof 2003, Heinz et al. 1992, Pizzol et al. 2010) in order to obtain information on population changes throughout the growing season to help time insecticide applications (Binns and Nyrop 1992, Heinz et al. 1992, Schmidt and Frey 1995). Information gained from scouting is intended to be used to target the most-susceptible life stages so as to reduce insecticide inputs, which consequently could decrease the potential for insecticide resistance. However, no quantitative information indicates that scouting reduces insecticide resistance under greenhouse conditions. Nonetheless, scouting at least provides a quantitative assessment of the population dynamics occurring in the greenhouse, both spatially and temporally (Cloyd and Sadof 2003, Pizzol et al. 2010). In addition, scouting not only involves the use of sticky cards but also visual inspection of the crop to determine the presence of larvae on plant parts (leaves and flowers).

Thresholds are a means to determine the extent of western flower thrips populations during the growing season and ascertain the level or number of western flower thrips that warrant the need to implement measures to avoid damage (Peck and Ellner 1997). Thresholds indicate that western flower thrips can be tolerated at some level, which may reduce the frequency of insecticide applications and consequently resistance (Cloyd and Sadof 2003, Peck and Ellner 1997). However, thresholds can vary depending on the specific crop. For example, thresholds range from 20 to 50 western flower thrips adults captured on sticky cards per week, with variability based on different crop types including rose (*Rosa* spp.), carnation (*Dianthus caryophyllus* L.), and strawberry (*Fragaria* × *ananassa* Duchesne ex Weston) (Casey and Parrella 2002, Cloyd and Sadof 2003, Steiner and Goodwin 2005). Thresholds may indicate that spray applications of insecticides are not required during certain times of the year due to low numbers of western flower thrips, which may lessen the potential for western flower thrips populations to develop resistance to insecticides (Cloyd and Sadof 2003, Nyrop et al. 1999). Thresholds may be more practical when crops are less susceptible to the viruses transmitted by western flower thrips whereas the use of thresholds may not be feasible for virus-sensitive crops because adult western flower thrips may be transmitting viruses. In this case, insecticide use may be intensified in order to suppress western flower thrips populations to low levels, consequently enhancing the development of resistance.

Insecticide rotations. Insecticide rotation is the temporal alternation of insecticides that have different modes of action (Immaraju et al. 1990). One of the primary means of alleviating resistance or mitigating the potential for western flower thrips populations developing insecticide resistance, and consequently extending the effectiveness of currently available insecticides, is rotating insecticides with different modes of action (Roush 1989, Robb and Parrella 1995). However, the rotation of insecticides with distinct modes of action will only be effective in delaying resistance if the insecticides applied select for different resistance mechanisms (Jensen 2000a). General recommendations include rotating different modes of action every 2–3 weeks or within a generation (Cloyd 2009a), although this depends on the time of year and ambient air temperatures in the greenhouse because development of the life cycle is contingent on temperature (Gaum et al. 1994, Lublinkhof and Foster 1977). In fact, higher temperatures can result in faster population growth, which can lead to increased insecticide applications, consequently enhancing the frequency of resistance (Peck and Ellner 1997). The concept is to use one mode of action within a generation, early in the crop production cycle, and then switch to a different mode of action in subsequent generations (Herron and Cook 2002). Therefore, the ideal situation is to utilize a multitude of insecticides with different modes of action (Jensen 2000a). Insecticide rotations have been reported to be more effective than insecticide mixtures (discussed below) (Immaraju et al. 1990), although this has not always been the case (Skylakakis 1981).

A potential problem associated with insecticide rotations is that western flower thrips populations may evolve different resistance mechanisms to the same insecticide (Bielza 2008). Furthermore, if cross-resistance occurs in a western flower thrips population, then rotating insecticides with different modes of action will not be effective in mitigating resistance (Comins 1986, Mani 1985). The rotation of insecticides with distinct modes of action is based on the assumption that the frequency or proportion of individuals in a western flower thrips population resistant to one insecticide will be reduced when an alternative insecticide with a different mode of action is applied (Hoy 1998, Mallet 1989, Mani 1985). Consequently, the frequency of resistant individuals declines in subsequent generations in which the initial insecticide is not applied. As such, when the first insecticide is reapplied there is a high frequency of susceptible individuals to the initial insecticide used as compared to insecticides that are applied afterward (Georghiou 1980). Therefore, the initial insecticide will provide effective suppression of a western flower thrips population when reintroduced into the rotation program (Mani 1985, Yu 2008). Rotating insecticides with different modes of action will reduce selection pressure as opposed to using only one insecticide (Brodsgaard 1994), resulting in exposure of individual western flower thrips to only one mode of action during their lifetime. Also, rotating insecticides with different modes of action is important in preserving existing insecticide products as well as in effectively managing western flower thrips populations (Denholm and Rowland 1992, Loughner et al. 2005). A factor, however, that may influence insecticide rotations is the stability of resistance, where resistance to certain insecticides may be retained in future generations despite rotating different modes of action (Georghiou and Taylor 1986). Therefore, rotation programs need to include a number of insecticides with different modes of action and also select for different resistance mechanisms (Dekeyser 2005).

Insecticide mixtures. Because greenhouse producers not only have to contend with western flower thrips but also other insect and/or mite pests, they will mix or combine pesticides (e.g., insecticides and miticides). These pesticide mixtures are designed to broaden the spectrum of activity and subsequently suppress multiple insect and mite pest populations including aphids, mealybugs, mites, whiteflies, and thrips (Cloyd 2009b, Warnock and Cloyd 2005). Insecticide mixtures may suppress resistant genes or alleles that are recessive, consequently leading to resistance to only one insecticide. However, insecticide mixtures may actually select for dominant genes/alleles that confer cross-resistance (Tabashnik 1989). The rate of resistance development in a western flower thrips population to two or more insecticides in a mixture may be delayed compared to applying the insecticides separately (National Research Council 1986), although resistance to an insecticide mixture may occur at a similar rate compared to separate applications of insecticides (Kable and Jeffery 1980). Studies have determined the efficacy of insecticide mixtures against populations of western flower thrips. For example, Warnock and Cloyd (2005) found that all two, three, and four-way combinations of spinosad with the other insecticides and miticides evaluated (e.g., abamectin, azadirachtin, bifenazate, and imidacloprid) did not influence the efficacy of spinosad in suppressing western flower thrips populations. In addition, Willmott et al. (2013) and Cloyd and Raudenbush (2014) demonstrated that all binary insecticide and miticide mixtures evaluated, which involved many different pesticides, provided approximately 80% mortality of western flower thrips. It is important to note that mixtures will only be effective in alleviating or mitigating resistance if the insecticides used have similar persistence (residual activity) and the western flower thrips populations do not exhibit any cross-resistance to the insecticides used in the mixture (Forgash 1984, Mani 1985, Tabashnik 1989).

Alternative insecticides. The use of alternative insecticides with broad-spectrum modes of action may help to alleviate problems associated with insecticide resistance in western flower thrips populations. Alternative insecticides include entomopathogenic fungi, insect growth regulators, and plant-derived essential oils.

Entomopathogenic fungi are typically applied as sprays to the plant leaves and may reduce selection pressure due to the unique mode of action by which they induce insect mortality. In general, fungal spores germinate and hyphae penetrate the insect cuticle by enzymatic degradation and mechanical pressure (Gillespie and Claydon 1989, Clarkson and Charnley 1996) and then consumption of internal tissues occurs (Hall et al. 1984). Mortality is typically dose-dependent, with higher spore concentrations resulting in quicker kill and higher mortality of insects (Vestergaard et al. 1995, James et al. 1998). The larvae and adult life stages are susceptible to infection by entomopathogenic fungi (Ansari et al. 2007); however, adults are more susceptible to infection than are larvae (Vestergaard et al. 1995, Maniania et al. 2001, Shipp et al. 2003). The entomopathogenic fungi, *Beauveria bassiana* (Bals.) Vuill., *Isaria fumosoroseus* (Wize) Brown & Smith (formerly *Paecilomyces fumosoroseus*), and *Metarhizium anisopliae* (Metschnikoff), can be substituted for standard insecticides (Murphy et al. 1998), which may diminish or mitigate resistance (Maniania et al. 2001). For instance, Kivett et al. (2015) demonstrated that rotation programs that involve entomopathogenic organisms, such as entomopathogenic fungi (*B. bassiana*, *M. anisopliae*, and *I. fumosoroseus*) and a bacterium (*Chromobacterium subtsugae* Martin), were just as effective as, and less costly than, rotation programs that rely on standard insecticides (e.g., spinosad, abamectin, pyridalyl, and chlorfenapyr). The use of entomopathogenic fungi will be most effective when western flower thrips populations are at low densities and when integrated with noninsecticidal strategies (Maniania et al. 2001).

Insect growth regulators are chemical compounds that disrupt the molting process or modify insect growth and development, thus leading to insect death (Yu 2008). Insect growth regulators, applied as either foliar sprays or drenches to the growing medium, have had limited use against western flower thrips. The main reason for the minimal use of insect growth regulators against western flower thrips is that most insect growth regulators are only directly active on the larval stage, not on the adults (Dhadialla et al. 1998, Ware 2005). Ascher et al. (1992) found that exposure to the insect growth regulator, azadirachtin, did not have any effect on adult female mortality or reduce female fecundity, and there were no effects on the larvae. However, Thoeming et al. (2003) reported that azadirachtin, when applied to the growing medium, may have systemic activity against the larvae with mortality between 70% and 90%. The insect growth regulators, diflubenzuron and pyriproxyfen, when applied to the growing medium to target the pupae, resulted in a substantial reduction in the emergence of western flower thrips adults (Ludwig and Oetting 2001). Studies have shown that mixing an insect growth regulator such as azadirachtin with another insecticide that includes an entomopathogenic fungus (*B. bassiana*) has synergistic effects against western flower thrips (R.A.C. unpubl.

data). However, under laboratory conditions, there was no evidence of any synergistic effects when azadirachtin was combined with certain entomopathogenic fungi including *B. bassiana* and *I. fumosoroseus* (Kivett unpubl. data). The use of insect growth regulators may help to mitigate insecticide resistance in western flower thrips populations if they are applied early in the production cycle before overlapping generations and different life stages (eggs, larvae, pupae, and adults) are present simultaneously.

Plant-derived essential oils are obtained by means of steam distillation from aromatic plants with products developed from several botanical sources (Koul et al. 2008). Certain plant-derived essential oils have been shown to act as repellents against western flower thrips (Picard et al. 2012); however, commercially available products based on rosemary, peppermint, cinnamon, clove oil, and garlic extract demonstrated minimal contact activity against western flower thrips, with an overall mortality $<30\%$ (Cloyd et al. 2009). Furthermore, a number of plant-derived essential oils are phytotoxic to many plants (Hollingsworth 2005, Isman 1999). Therefore, the low mortality and potential for phytotoxicity suggests that the use of plant-derived essential oils will not be a feasible option to greenhouse producers in mitigating insecticide resistance.

Conclusion and Future Research Efforts

Insecticides will continue to be used to suppress western flower thrips populations in order to maintain the aesthetics of high-value horticultural and ornamental crops (Gao et al. 2012) as well as the fact that western flower thrips vector a number of tospoviruses (Allen and Broadbent 1986, Pappu et al. 2009). However, problems associated with the introduction of new insecticides for use against western flower thrips populations in greenhouse production systems are the costs and regulations of registering a new active ingredient, subsequently resulting in fewer new active ingredients being introduced into the marketplace against western flower thrips (Lewis 1977, Reitz and Funderburk 2012). In fact, there is the possibility that no new active ingredients will be added to the existing array of insecticides. Nevertheless, greenhouse producers need to exercise caution and judiciously use insecticides in order to prolong their effectiveness (Nauen and Denholm 2005). Although resistance may be a contributing factor responsible for inadequate suppression of western flower thrips populations, failures can also be attributed to insufficient spray coverage or improper timing of applications (Shelton et al. 2006).

Greenhouse producers should assume that populations of western flower thrips in greenhouses are resistant to one or more insecticides. Nevertheless, it is important to rotate insecticides with different modes of action and use insecticides with broad modes of activity in order to reduce the frequency of resistant genes or alleles within a western flower thrips population (Georghiou 1994). Proper rotation programs need to be implemented that do not over-use the same mode of action in order to preserve the effectiveness of existing insecticide products by abiding with the IRAC (Insecticide Resistance Action Committee, http://www.irac-online.org; accessed November 2015) label designations. Moreover, most insecticide labels contain resistance management information in order to curtail the advent of resistance, thus preserving the effectiveness of existing products. For example, the Conserve (active ingredient = spinosad) label states the following:

> "Do not make more than two consecutive applications of Group 5 insecticides. If additional treatments are required after two consecutive applications of Group 5 insecticides, rotate to another class of effective insecticides for at least one application."

However, the sole use of insecticides against western flower thrips is not a sustainable strategy. Therefore, it is important that greenhouse producers implement noninsecticidal strategies (e.g., sanitation, screening, and biological control) in order to reduce the input of insecticides and consequently the selection pressure placed on western flower thrips populations.

Current and future research efforts associated with western flower thrips management in greenhouse production systems include: (a) using multiple biological control agents (Ebssa et al. 2006, Premachandra et al. 2003, Saito and Brownbridge 2016), and (b) integrating insecticides with biological control agents (Messelink et al. 2014, Saito and Brownbridge 2016, Thoeming and Poehling 2006). Both of these strategies are designed to reduce insecticide inputs, thus diminishing selection pressure placed on western flower thrips populations, and to decreasing insecticide resistance.

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References Cited

Allen, R. and A.B. Broadbent. 1986. Transmission of tomato spotted wilt virus in Ontario greenhouses by *Frankliniella occidentalis*. Can. J. Plant Pathol. 8: 33–38.

Allen, W.R., B. Tehrani and R. Luft. 1993. Effect of horticultural oil, insecticidal soap, and film-forming products on the western flower thrips and the tomato spotted wilt virus. Plant Dis. 77: 915–918.

Ansari, M.A., F.A. Shah, M. Whittaker, M. Prasad and T.M. Butt. 2007. Control of western flower thrips (*Frankliniella occidentalis*) pupae with *Metarhizium anisopliae* in peat and peat alternative growing media. Biol. Control 40: 293–297.

Argentine, J.A., J.M. Clarck and D.N. Ferro. 1989. Relative fitness of insecticide resistant Colorado potato beetle strains (Coleoptera: Chrysomelidae). Environ. Entomol. 18: 705–710.

Ascher, K.R.S., M. Klein and J. Meisner. 1992. Azatin, a neem formulation, acts on nymphs of the western flower thrips. Phytoparasitica 20: 305–306.

Bielza, P. 2008. Insecticide resistance management strategies against the western flower thrips, *Frankliniella occidentalis*. Pest Manag. Sci. 64: 1131–1138.

Bielza, P., V. Quinto, C. Graválos, J. Abellán and E. Fernández. 2008. Lack of fitness costs of insecticide resistance in the western flower thrips (Thysanoptera: Thripidae). J. Econ. Entomol. 101: 499–503.

Bielza, P., V. Quinto, J. Contreras, M. Torné, A. Martin and P.J. Espinosa. 2007. Resistance to spinosad in the western flower thrips, *Frankliniella occidentalis* (Pergande), in greenhouses of south-eastern Spain. Pest Manag. Sci. 63: 682–687.

Binns, M.R. and J.P. Nyrop. 1992. Sampling insect populations for the purpose of IPM decision making. Annu. Rev. Entomol. 37: 427–453.

Broadbent, A.B. and D.J. Pree. 1997. Resistance to insecticides in populations of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) from greenhouses in the Niagara region of Ontario. Can. Entomol. 129: 907–913.

Brodsgaard, H.F. 1989. *Frankliniella occidentalis* (Thysanoptera: Thripidae)—A new pest in Danish greenhouses. Tidsskrift for Planteavl 93: 83–91.

Brodsgaard, H.F. 1994. Insecticide resistance in European and African strains of western flower thrips (Thysanoptera: Thripidae) tested in a new residue-on-glass test. J. Econ. Entomol. 87: 1141–1146.

Carrière, Y. 2003. Haplodiploidy, sex, and the evolution of pesticide resistance. J. Econ. Entomol. 96: 1626–1640.

Casey, C. and M. Parrella. 2002. Demonstration and implementation of a reduced risk pest management strategy in fresh cut flowers. IOBC/WPRS Bull. 25: 45–48.

Childers, C.C. 1997. Feeding and oviposition injuries to plants, Pp. 505–537. *In* Lewis T. (ed.), Thrips as Crop Pests. CAB International, New York, NY.

Chisholm, I.F. and T. Lewis. 1984. A new look at thrips (Thysanoptera) mouthparts, their action and effects of feeding on plant tissue. Bull. Entomol. Res. 74: 663–675.

Clarkson, J.M. and A.K. Charnley. 1996. New insights into the mechanisms of fungal pathogenesis in insects. Trends Microbiol. 4: 197–203.

Cloyd, R.A. 2009a. Western flower thrips (*Frankliniella occidentalis*) management on ornamental crops grown in greenhouses: Have we reached an impasse? Pest Technol. 3: 1–9.

Cloyd, R.A. 2009b. Getting mixed-up: Are greenhouse producers adopting appropriate pesticide mixtures to manage arthropod pests? HortTechnology 19: 638–646.

Cloyd, R.A. 2015. Western flower thrips management in greenhouse production systems in the 21st Century: Alternative strategies need to be considered. Acta Hort. 1104: 381–394.

Cloyd, R.A., C.L. Galle, S.R. Keith, N.A. Kalscheur and K.E. Kemp. 2009. Effect of commercially available plant-derived essential oil products on arthropod pests. J. Econ. Entomol. 102: 1567–1579.

Cloyd, R.A. and A.L. Raudenbush. 2014. Efficacy of binary pesticide mixtures against western flower thrips. HortTechnology 24: 449–456.

Cloyd, R.A. and C.S. Sadof. 2003. Seasonal abundance and use of action threshold for western flower thrips, in a cut carnation greenhouse. HortTechnology 13: 497–500.

Comins, H.N. 1986. Tactics for resistance management using multiple pesticides. Agric. Ecosyst. Environ. 16: 129–148.

Dekeyser, M.A. 2005. Acaricide mode of action. Pest Manag. Sci. 61: 103–110.

Denholm, I., M. Cahill, T. J. Dennehy and A.R. Horowitz. 1998. Challenges with managing insecticide resistance in agricultural pests, exemplified by the whitefly, *Bemisia tabaci*. Phil. Tran. Royal Soc. London, Series B 353: 1757–1767.

Denholm, I. and J.B. Jespersen. 1998. Insecticide resistance management in Europe: Recent developments and prospects. Pest. Sci. 52: 193–195.

Denholm, I. and M.W. Rowland. 1992. Tactics for managing pesticide resistance in arthropods: Theory and practice. Ann. Rev. Entomol. 37: 91–112.

Dhadialla, T.S., G.R. Carlson and D.P. Le. 1998. New insecticides with ecdysteroidal and juvenile hormone activity. Annu. Rev. Entomol. 43: 545–569.

Diabate, A., T. Baldet, F. Chandre, M. Akoobeto, T.R. Guiguemde, F. Darriet, C. Brengues, P. Guillet, J. Hemingway, G.J. Small and J.M. Hougard. 2002. The role of agricultural use of insecticides in resistance to pyrethroids in *Anopheles gambiae* s.l. in Burkina Faso. Am. J. Trop. Med. Hyg. 67: 617–622.

Ebssa, L., C. Borgemeister, O. Berndt and H.M. Poehling. 2006. Simultaneous application of entomopathogenic nematodes and predatory mites to control western flower thrips, *Frankliniella occidentalis*. Biol. Control 39: 66–74.

Espinosa, P.J., J. Contreras, V. Quinto, C. Grávalos, E. Fernández and P. Bielza. 2005. Metabolic mechanisms of insecticide resistance in the western flower thrips, *Frankliniella occidentalis* (Pergande). Pest Manag. Sci. 61: 1009–1015.

Ferrari, J.A. and G.P. Georghiou. 1981. Effects on insecticidal selection and treatment on reproductive potential of resistance, susceptible, and heterozygous strains of the southern house mosquito. J. Econ. Entomol. 74: 323–327.

ffrench-Constant, R.H. and R.T. Roush. 1990. Resistance detection and documentation: The relative roles of pesticidal and biochemical assays, Pp. 4–38. *In* Pesticide Resistance in Arthropods. Chapman & Hall, New York, NY.

Forgash, A.J. 1984. History, evolution, and consequences of insecticide resistance. Pestic. Biochem. Physiol. 22: 178–186.

Gao, Y., Z. Lei and S.R. Reitz. 2012. Western flower thrips resistance to insecticides: Detection, mechanism and management strategies. Pest Manag. Sci. 68: 1111–1121.

Gaum, W.G., J.H. Giliomee and K.L. Pringle. 1994. Life history and life tables of western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), on English cucumbers. Bull. Entomol. Res. 84: 219–224.

Georghiou, G.P. 1980. Insecticide resistance and prospects for its management, Pp. 131–145. *In* Gunther, F.A. (ed.), Residue Reviews, Vol. 76. Springer-Verlag, New York.

Georghiou, G.P. 1986. The magnitude of the resistance problem, Pp. 14–43. *In* Pesticide Resistance: Strategies and Tactics for Management. National Academy of Sciences, Washington, DC.

Georghiou, G.P. 1994. Principles of insecticide resistance management. Phytoprotection 75: 51–59.

Georghiou, G.P. and C.E. Taylor. 1977. Genetic and biological influences in the evolution of insecticide resistance. J. Econ. Entomol. 70: 319–323.

Georghiou, G.P. and C.E. Taylor. 1986. Factors influencing the evolution of resistance, Pp. 157–169. *In* Pesticide Resistance: Strategies and Tactics for Management, National Research Council, National Academy Press, Washington, DC.

Gerin, C., T.H. Hance and G. Van Impe. 1994. Demographical parameters of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). J. Appl. Entomol. 118: 370–377.

Gerin, C., T.H. Hance and G. Van Impe. 1999. Impact of flowers on the demography of western flower thrips *Frankliniella occidentalis* (Thysan., Thripidae). J. Appl. Entomol. 123: 569–574.

Gillespie, A.T. and N. Claydon. 1989. The use of entomogenous fungi for pest control and the role of toxins in pathogenesis. Pest. Sci. 27: 203–215.

Hall, R.A., A.T. Gillespie and H.D. Burges. 1984. Use of fungi as microbial insecticides. Ann. Report Glasshouse Crops Res. Inst. 98–103.

Hansen, E.A., J.E. Funderburk, S.R. Reitz, S. Ramachandran, J.E. Eger and H. McAuslane. 2003. Within-plant distribution of *Frankliniella* species (Thysanoptera: Thripidae) and *Orius insidiosus* (Heteroptera: Anthocoridae) in field pepper. Environ. Entomol. 32: 1035–1044.

Harrewijn, P., W.F. Tjallingii and C. Mollema. 1996. Electrical recording of plant penetration by western flower thrips. Entomol. Exp. Appl. 79: 345–353.

Heinz, K.M., M.P. Parrella and J.P. Newman. 1992. Time-efficient use of yellow sticky traps in monitoring insect populations. J. Econ. Entomol. 85: 2263–2269.

Helyer, N.L. and P.J. Brobyn. 1992. Chemical control of western flower thrips (*Frankliniella occidentalis* Pergande). Ann. Appl. Biol. 121: 219–231.

Herron, G.A. and D.F. Cook. 2002. Initial verification of the resistance management strategy for *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) in Australia. Aust. J. Entomol. 41: 187–191.

Herron, G.A. and G.C. Gullick. 2001. Insecticide resistance in Australian populations of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) causes the abandonment of pyrethroid chemicals for its control. Gen. Appl. Entomol. 30: 21–26.

Herron, G.A. and T.M. James. 2005. Monitoring insecticide resistance in Australian *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) detects fipronil and spinosad resistance. Aust. J. Entomol. 44: 299–303.

Hollingsworth, R.G. 2005. Limonene, a citrus extract, for control of mealybugs and scale insects. J. Econ. Entomol. 98: 772–779.

Hou, W., Q. Liu, L. Tian, Q. Wu, Y. Zhang, W. Xie, S. Want, San Miguel, K. J. Funderburk and G. Scott. 2014. The $\alpha 6$ nicotinic acetylcholine receptor subunit of *Frankliniella occidentalis* is not involved in resistance to spinosad. Pest. Biochem. Physiol. 111: 60–67.

Hoy, M.A. 1998. Myths, models and mitigation of resistance to pesticides. Phil. Trans. Royal Soc. London. Biol. Sci. 353: 1787–1795.

Hussey, N.W. 1965. Possibilities for integrated control of some glasshouse pests. Ann. Appl. Biol. 56: 347–350.

Immaraju, J.A., J.G. Morse and R.F. Hobz. 1990. Field evaluation of insecticide rotation and mixtures as strategies for citrus thrips (Thysanoptera: Thripidae) resistance management in California. J. Econ. Entomol. 83: 306–314.

Immaraju, J.A., T.D. Paine, J.A. Bethke, K.L. Robb and J.P. Newman. 1992. Western flower thrips (Thysanoptera: Thripidae) resistance to insecticides in coastal California greenhouses. J. Econ. Entomol. 85: 9–14.

Isman, M.B. 1999. Pesticides based on plant essential oils. Pesticide Outlook 4: 68–72.

James, R.R., B. Croft, B. Shaffer and B. Lighthart. 1998. Impact of temperature and humidity on host–pathogen interactions between *Beauveria bassiana* and a coccinellid. Environ. Entomol. 27: 1506–1513.

Jensen, S.E. 1998. Acetylcholinesterase activity associated with methiocarb resistance in a strain of western flower thrips, *Frankliniella occidentalis* (Pergande). Pestic. Biochem. Physiol. 61: 191–200.

Jensen, S.E. 2000a. Insecticide resistance in the western flower thrips, *Frankliniella occidentalis*. Integ. Pest Manag. Rev. 5: 131–146.

Jensen, S.E. 2000b. Mechanisms associated with methiocarb resistance in *Frankliniella occidentalis* (Thysanoptera: Thripidae). J. Econ. Entomol. 93: 464–471.

Kable, P.F. and H. Jeffery. 1980. Selection for tolerance in organisms exposed to sprays of biocide mixtures. A theoretical model. Phytopathol. 70: 8–12.

Kirk, W.D.J. and L.I. Terry. 2003. The spread of the western flower thrips, *Frankliniella occidentalis* (Pergande). Agric. Forest Entomol. 5: 301–310.

Kivett, J.M., R.A. Cloyd and N.M. Bello. 2015. Insecticide rotation program with entomopathogenic organisms for suppression of western flower thrips (Thysanoptera: Thripidae) adult populations under greenhouse conditions. J. Econ. Entomol. 108: 1936–1946.

Kontsedalov, S., P.G. Weintraub, A.R. Horowitz and I. Ishaaya. 1998. Effects of insecticides on immature and adult western flower thrips (Thysanoptera: Thripidae) in Israel. J. Econ. Entomol. 91: 1067–1071.

Koul, O., S. Walia and G.S. Dhaliwal. 2008. Essential oils as green pesticides: Potential and constraints. Biopestic. Int. 4: 63–84.

Lewis, C.J. 1977. The economics of pesticide research, Pp. 237–245. *In* Cherrett, J.M. and Sager, G.R. (eds.). Origins of Pest Parasite, Disease and Weed Problems. Blackwell, Oxford, U.K.

Lewis, T. 1997. Pest thrips in perspective, Pp. 1–14. *In* Lewis, T. (ed.), Thrips as Crop Pests. CAB International, Wallingford, U.K.

Li, X., M.A. Schuler and M.R. Berenbaum. 2007. Molecular mechanisms of metabolic resistance to synthetic and natural xenobiotics. Annu. Rev. Entomol. 52: 231–253.

Loughner, R.L., D.F. Warnock and R.A. Cloyd. 2005. Resistance of greenhouse, laboratory, and native populations of western flower thrips to spinosad. HortScience 40: 146–149.

Lublinkhof, J. and D.E. Foster. 1977. Development and reproductive capacity of *Frankliniella occidentalis* (Thysanoptera: Thripidae) reared at three temperatures. J. Kansas Entomol. Soc. 50: 313–316.

Ludwig, S.W. and R.D. Oetting. 2001. Evaluation of medium treatments for management of *Frankliniella occidentalis* (Thripidae: Thysanoptera) and *Bradysia coprophila* (Diptera: Sciaridae). Pest Manag. Sci. 57: 1114–1118.

Mallet, J. 1989. Evolution of insecticide resistance: Have the insects won? Tree 4: 336–340.

Mani, G.S. 1985. Evolution of resistance in presence of two insecticides. Genetics 109: 761–783.

Maniania, N.K., S. Ekesi, B. Löhr and F. Mwangi. 2001. Prospects for biological control of the western flower thrips, *Frankliniella occidentalis*, with the entomopathogenic fungus, *Metarhizium anisopliae*, on chrysanthemum. Mycopathologia 155: 229–235.

Martin, N.A. and P.J. Workman. 1994. Confirmation of a pesticide-resistant strain of western flower thrips in New Zealand. Pp. 144–148. *In* Proc. 47th NZ Plant Protect. Conf.

Maymo, A.C., A. Cervera, R. Sarabia, R. Martínez-Pardo and M. Dolores Garcerá. 2002. Evaluation of metabolic detoxifying enzyme activities and insecticide resistance in *Frankliniella occidentalis*. Pest Manag. Sci. 58: 928–934.

Messelink, G.J., J. Bennison, O. Alomar, B.L. Ingegno, L. Tavella, L. Shipp, E. Palevsky and F.L. Wäckers. **2014.** Approaches to conserving natural enemy populations in greenhouse crops: Current methods and future prospects. BioControl 59: 377–393.

Mound, L.A. 1996. The Thysanoptera vector species of tospoviruses. Acta. Hort. 431: 298–309.

Murphy, B.C., T.A. Morisawa, J.P. Newman, S.A. Tjosvold and M.P. Parrella. 1998. Fungal pathogen controls thrips in greenhouse flowers. California Agric. 52: 32–36.

National Research Council. **1986.** Tactics for prevention and management, Pp. 313–326. *In* Pesticide Resistance: Strategies and Tactics for Management. National Academy Press, Washington, DC.

Nauen, R. and I. Denholm. 2005. Resistance of insect pests to neonicotinoid insecticides: Current status and future prospects. Arch. Insect Biochem. Physiol. 58: 200–215.

Nyrop, J.P., M.R. Binns and W. van der Werf. 1999. Sampling for IPM decision making: Where should we invest time and resources? Phytopathology 89: 1104–1111.

Pappu, H.R., R.A.C. Jones and R.K. Jain. 2009. Global status of tospovirus epidemics in diverse cropping systems: Success achieved and challenges ahead. Virus Res. 141: 219–236.

Parrella, M.P. 1995. IPM: Approaches and prospects, Pp. 357–363. *In* Parker, B.L., Skinner, M. and Lewis T. (eds.). Thrips Biology and Management, Plenum Press, New York, NY.

Parrella, M.P. and B. Murphy. 1996. Western flower thrips: identification, biology and research on the development of control strategies. Bull. IOBC/WPRS (OILB/SROP) 19: 115–118.

Peck, S.L. and S.P. Ellner. 1997. The effect of economic thresholds and life-history parameters on the evolution of pesticide resistance in a regional setting. Am. Nat. 149: 43–63.

Picard, I., R.G. Hollingsworth, S. Salmieri and M. Lacroix. 2012. Repellency of essential oils to *Frankliniella occidentalis* (Thysanoptera: Thripidae) as affected by type of oil and polymer release. J. Econ. Entomol. 105: 1238–1247.

Pizzol, J., D. Nammour, P. Hervouet, A. Bout, N. Desneux and L. Mailleret. 2010. Comparison of two methods of monitoring thrips populations in a greenhouse rose crop. J. Pest. Sci. 83: 191–196.

Premachandra, D.W.T.S., C. Borgemeister, O. Berndt, R.U. Ehlers and H.M. Poehling. 2003. Laboratory bioassays of virulence of entomopathogenic nematodes against soil-inhabiting stages of *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae). Nematology 5: 539–547.

Race, S.R. 1961. Early-season thrips control on cotton in New Mexico. J. Econ. Entomol. 54: 974–976.

Reitz, S.R. 2009. Biology and ecology of the western flower thrips (Thysanoptera: Thripidae): The making of a pest. Florida Entomol. 92: 7–13.

Reitz, S.R. and J. Funderburk. 2012. Management strategies for western flower thrips and the role of insecticides, Pp. 355–384. *In* Perveen, F. (ed.). Agricultural and Biological Sciences: Insecticides—Pest Engineering. InTech, Rijeka, Croatia.

Reitz, S.R., E.L. Yearby, J.E. Funderburk, J. Stavisky, M.T. Momol and S.M. Olson. 2003. Integrated management tactics for *Frankliniella* thrips (Thysanoptera: Thripidae) in field-grown pepper. J. Econ. Entomol. 96: 1201–1214.

Robb, K.L. 1989. Analysis of *Frankliniella occidentalis* (Pergande) as a pest of floricultural crops in California greenhouses. Ph.D. Dissertation. Univ. California, Riverside, CA.

Robb, K.L. and M.P. Parrella. 1995. IPM of western flower thrips, Pp. 365–370. *In* Parker, B L., Skinner, M. and Lewis T. (eds.), Thrips Biology and Management. Plenum Press, New York.

Roush, R.T. 1989. Designing resistance management programs: How can you choose? Pestic. Sci. 26: 423–441.

Roush, R.T. 1993. Occurrence, genetics and management of insecticide resistance. Parasitol. Today 9: 174–179.

Roush, R.T. and J.C. Daly. 1990. The role of population genetics in resistance research and management, Pp. 97–152. *In*: R. T. Roush and B. E. Tabashnik (eds.). Pesticide Resistance in Arthropods, Chapman and Hall, New York, NY.

Roush, R.T. and J.A. McKenzie. 1987. Ecological genetics of insecticide and acaricide resistance. Annu. Rev. Entomol. 32: 361–380.

Saito, T. and M. Brownbridge. 2016. Compatibility of soil-dwelling predators and microbial agents and their efficacy in controlling soil-dwelling stages of western flower thrips *Frankliniella occidentalis*. Biol. Control 92: 92–100.

Schmidt, M.E. and J.E. Frey. 1995. Monitoring of the western flower thrips *Frankliniella occidentalis* in greenhouses. Med. Fac. Landbouww. Univ. Gent 60: 84–87.

Shelton, A.M., J.Z. Zhao, B.A. Nault, J. Plate, F.R. Musser and E. Larentzaki. 2006. Patterns of insecticide resistance in onion thrips (Thysanoptera: Thripidae) in onion fields in New York. J. Econ. Entomol. 99: 1798–1804.

Shipp, J.L., Y. Zhang, W.A. Hunt and G. Ferguson. 2003. Influence of humidity and greenhouse microclimate on the efficacy of *Beauveria bassiana* (Balsamo) for control of greenhouse arthropod pests. Environ. Entomol. 32: 1154–1163.

Skylakakis, G. 1981. Effects of alternating and mixing pesticides on the build-up of fungal resistance. Phytopathology 71: 1119–1121.

Soderland, D.M. and J.R. Bloomquist. 1990. Molecular mechanisms of insecticide resistance, Pp. 58–96. *In* Roush, R.T. and Tabashnik B.E. (eds.), Pesticide Resistance in Arthropods. Chapman and Hall, New York.

Steiner, M.Y. and S. Goodwin. 2005. Management of western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) in hydroponic strawberry crops: Using yellow sticky traps to determine action thresholds. Aust. J. Entomol. 44: 288–292.

Tabashnik, B.E. 1989. Managing resistance with multiple pesticide tactics: Theory, evidence, and recommendations. J. Econ. Entomol. 82: 1263–1269.

Thoeming, G. and H.M. Poehling. 2006. Integrating soil-applied azadirachtin with *Amblyseius cucumeris* (Acari: Phytoseiidae) and *Hypoaspis aculeifer* (Acari: Laelapidae) for the management of *Frankliniella occidentalis* (Thysanoptera: Thripidae). Environ. Entomol. 35: 746–756.

Thoeming, G., C. Borgemeister, M. Sétamou and H.M. Poehling. 2003. Systemic effects of neem on western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae). J. Econ. Entomol. 96: 817–825.

Vestergaard, S., A. Gillespie, T. Butt, G. Schreiter and J. Eilenberg. 1995. Pathogenicity of the hyphomycete fungi *Verticillium lecanii* and *Metarhizium anisopliae* to the western flower thrips, *Frankliniella occidentalis*. Biocontrol Sci. Technol. 5: 185–192.

Ware, G.W. 2005. Complete Guide to Pest Control With and Without Chemicals. 4th ed. MeisterPro Information Resources, Willoughby, OH.

Warnock, D.F. and R.A. Cloyd. 2005. Effect of pesticide mixtures in controlling western flower thrips (Thysanoptera: Thripidae). J. Entomol. Sci. 40: 54–66.

Weiss, A., J.E. Dripps and J. Funderburk. 2009. Assessment of implementation and sustainability of integrated pest management programs. Florida Entomol. 92: 24–28.

Wijkamp, I., N. Alarza, R. Goldback and D. Peters. 1995. Distinct levels of specificity in thrips transmission of tospoviruses. Phytopathology 85: 1069–1074.

Willmott, A.L., R.A. Cloyd and K. Yan Zhu. 2013. Efficacy of pesticide mixtures against the western flower thrips (Thysanoptera: Thripidae) under laboratory and greenhouse conditions. J. Econ. Entomol. 106: 247–256.

Yu, S.J. 2008. The Toxicology and Biochemistry of Insecticides. CRC Press, Boca Raton, FL.

Zhang, S.Y., S. Kono, T. Murai and T. Miyata. 2008. Mechanisms of resistance to spinosad in the western flower thrip, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). Insect Sci. 15: 125–132.

Zhao, G., W. Liu and C.O. Knowles. 1994. Mechanisms associated with diazinon resistance in western flower thrips. Pestic. Biochem. Physiol. 49: 13–23.

Zhao, G., W. Liu, and C.O. Knowles. 1995a. Mechanisms conferring resistance of western flower thrips to bendiocarb. Pestic. Sci. 44: 293–297.

Zhao, G., W. Liu, J.M. Brown, and C.O. Knowles. 1995b. Fenvalerate resistance mechanisms in western flower thrips (Thysanoptera: Thripidae). J. Econ. Entomol. 88: 531–535.

Zhao, G., W. Liu, J.M. Brown, and C.O. Knowles. 1995c. Insecticide resistance in field and laboratory strains of western flower thrips (Thysanoptera: Thripidae). J. Econ. Entomol. 88: 1164–1170.