Manipulating Whitefly Behaviour Using Plant Resistance, Reduced-Risk Sprays, Trap Crops and Yellow Sticky Traps for Improved Control for Sweet Pepper Greenhouse Crops

by

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Abstract

The greenhouse whitefly, *Trialeurodes vaporariorum* (Hemiptera, Aleyrodidae) has been identified as a priority pest for multiple vegetable and ornamental greenhouse crops. The deliberate manipulation of insect behaviour for the purpose of pest management is of great interest to greenhouse growers looking to reduce pesticide use in commercial sweet pepper (*Capsicum annuum)* greenhouses. In the following, alternative control tactics were individually evaluated in the laboratory and greenhouse to identify the greatest modifiers of *T. vaporariorum* settling and oviposition behaviours on peppers. The four tactics tested were plant resistance (PR), reduced-risk sprays (RRSs), trap crops (TCs) and yellow sticky traps (YSTs). The individual tactics that were most effective at reducing adult and egg populations on peppers were combined to determine if the simultaneous use of behaviour modifying tactics enhanced whitefly control.

Results indicated that the greatest modifiers of *T. vaporariorum* settling and oviposition behaviours on peppers were YSTs > TCs > RRSs > PR. Combining YSTs and TCs with RRRs indicated that *T. vaporariorum* settling and oviposition can be directed away from peppers to traps. Although whitefly settling was lowest on peppers in the TC + YST + RRS combination, there was no significant benefit of using three tactics (TC + YST + RRS) over two tactics (TC + YST). Trap crops used in combination with yellow sticky traps reduced adult densities on peppers by 53% and provided a more consistent and effective method of reducing whiteflies on peppers than using reduced-risk sprays. The use of YSTs + TCs is recommended as an alternative whitefly control tactic for sweet peppers. Implications of these findings in the context of whitefly host selection and as a potential greenhouse management strategy are discussed.

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Dedication

This thesis is affectionately dedicated to my partner in life, Jay Fox, who puts love in my heart and a smile on my face. And, to Betsy Mae Fox, who makes me believe in a bright and beautiful tomorrow.

Co-Authorship Statement

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Murray Isman provided concepts on information synthesis and contributed to the writing. I did the literature review and wrote the paper.

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Murray Isman provided identification of the concept and helped with the experimental design of the research. I designed the experiment, conducted the laboratory work, analyzed the statistics and wrote the paper.

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Chapter 1[*] Introduction and research objectives

1.1 Whiteflies (Hemiptera, Aleyrodidae)

Whiteflies are small, often inconspicuous insects' that are globally distributed as agricultural pests of both greenhouse and field crops. Although > 1,500 species of whiteflies exist, only a few cause serious economic losses. The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) and the sweet potato whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera, Aleyrodidae)*,* represent the two most widely studied and pestiferous species. Although the focus of this project was to study *T. vaporariorum,* information on both species is presented to provide a more comprehensive understanding of whitefly biology.

Their common name, whitefly, is due to the presence of white wax and lipid particles that cover the body and wings of most adult species (Byrne & Hadley, 1988; Buckner *et al.*, 1994). *Trialeurodes vaporariorum* and *B. tabaci* are polyphagous herbivores that reduce crop yields by extracting water, carbohydrates and amino acids from plant phloem (Lloyd, 1922). Both species can transmit plant viruses. However, serious viral diseases are more commonly associated with *B. tabaci* (Cohen, 1990). As phloem-feeing insects, whiteflies excrete sticky honeydew that can cover fruit and foliage of crops. Honeydew fosters the growth of sooty mold (*Cladosporium*) on plants and reduces plant photosynthesis (Lloyd, 1922; Hoddle *et al.*, 1998; Smith *et al.*, 2001).

1.1.1 Species classification and taxonomic position

Of the > 1,500 named whitefly species it is thought that this number represents only a small proportion of Aleyrodids in existence (Bink-Moenen, 1990; Martin, 2004). Most species are found in tropical and subtropical areas. However, some species are known to exist in all major agricultural regions of the world (Bink-Moenen, 1990). Based

[*]A version of this chapter will be submitted for publication. Moreau, T.L. and M.B. Isman. 2010. An overview of whitefly behavioural manipulation.

on the diversity of parasitoids in the Pakistan region, researchers have speculated that this is their centre of origin (Brown *et al.*, 1995). Whitefly systematics and classification are complicated because whitefly populations from distinct geographic locations demonstrate considerable variation in host plant preferences, morphology, life histories and even disease-transmission capacities (Bink-Moenen, 1990; Oliveira *et al.*, 2001). For this reason, some whitefly species (i.e. *B. tabaci)* with distinct populations are further divided into biotypes.

Whiteflies, in the order Hemiptera, constitute a single superfamily, the Aleyrodoidea, within the suborder Sternorrhyncha (Vondohlen & Moran, 1995; Martin *et al.*, 2000). Whiteflies belong to the single family, Aleyrodidae which is most closely related to the Psyllidae in that adults of both groups have two tarsal segments that are almost equal in size (Bink-Moenen, 1990). Aleyrodidae are physiologically unique due to the presence of a vasiform orifice, which is thought to function as a catapult to expel honeydew away from whitefly nymphs.

1.1.2 Life history

Hemipterans undergo hemimetabolous development that includes three distinct stages: egg, nymph and imago (adult). Historically, the terms nymph, larvae and pupa have been used to describe whitefly immatures. Technically, nymph is the correct terminology but pupa has been widely used to describe the last phase of the fourth instar and will be used here for consistency. Whitefly species classification is based on the last nymphal stage (referred to as the pupa, pupal case, 4th instar, puparium), rather than on the adult stage (Gill, 1990). *Trialeurodes vaporariorum* life cycle consists of six stages including the egg, the crawler (1st nymphal instar), two sessile nymph instars (2nd and 3rd instar), the pupa (which is further divided into three substages: the 4th instar, the prepupa and the pupa) and the adult or imago (Gill, 1990). During oviposition, eggs are often laid in a circular fashion and the female will continue to feed while rotating its rostrum to deposit eggs. Eggs are secured to the plant by a pedicel, which is a peglike extension of the chorion (Gill, 1990). The egg pedicel is either inserted into a slit in the leaf surface (made by the ovipositor) or into a stomata opening. In addition to securing the egg to the plant, the pedicle is thought to function as a water source for eggs (Byrne *et al.*, 1990).

The first instar, or crawler, is the only immature form that is mobile. The crawler has functional walking legs and antennae and moves short-distances (usually on the same leaf) from the site of egg hatching in search for feeding sites (Byrne & Bellows, 1991; Martin *et al.*, 2000). The duration and distance of crawler movement depends on the crawlers' ability to locate acceptable feeding sites. Second and third instar nymphs are sessile with no means of relocation even if a feeding site deteriorates. The fourth instar has been described as having three morphologically distinct forms (Nechols & Tauber, 1977). The early fourth instar is flat, translucent and feeds; the next form, the transitional substage, is expanded, waxy and has dorsal and lateral spinelike processes. The last and final stage of the fourth instar, when the pharate adult (within the cuticle of the previous stadium) is present, possesses red eyes and the yellow body pigment typical of adults. The term pupa describes the last non-feeding portion of the fourth instar found after apolysis has occurred. The two early forms of this last stadium (period between moults or intermoult period) are referred to as the fourth nymphal instars and the prepupa (Byrne & Bellows, 1991). Sexual dimorphism of the pupa can be recognized for some whitefly species where male puparia are smaller than females. In species that do not exhibit sexual dimorphism, it is not possible to determine the sex of individual pupa.

Adult *T. vaporariorum* emerge from their pupal case through an inverted T-slit in the dorsum. Typically, adult emergence occurs 1 – 4 h after sunrise (van Lenteren & Noldus, 1990). The teneral period for *B. tabaci* and *T. vaporariorum* is approximately 4 h at 27°C (Byrne & von Bretzel, 1987). Adults begin to feed immediately even before their wings have unfolded (Martin, 2004). Newly emerged adults have clear wings that are slowly covered with wax secreted from lateral abdominal glands (Byrne & Hadley, 1988). Very little whitefly movement and emergence occurs during the scotophase. Adult *B. tabaci* and *T. vaporariorum* can be distinguished visually by their shape. *Bemisia tabaci* adults appear smaller than *T. vaporariorum* and they hold their wings at a 'roof-like' angle (45° angle), whereas, *T. vaporariorum* have broader wings that are held nearly parallel to the leaf surface (Arno *et al.*, 2006). Adult sexual dimorphism is seen in differences in the genitalia, the number of ventral abdominal wax plates, the antennae and in the slightly smaller body size of males (Figure 1.1) (Hodges & Evans, 2005).

Figure 1.1. Adult female (left) and male (right) *Trialeurodes vaporariorum.*

1.1.3 Reproduction

Whitefly reproduction can be sexual or parthenogenetic (development from unfertilized eggs) (Martin *et al.*, 2000). *Trialeurodes vaporariorum* tend to show arrhenotokous parthenogenesis where unmated females lay haploid (male) eggs and mated females lay either haploid (male) or diploid (female) eggs. The courtship and mating behaviour of whiteflies differs between species and biotypes (Perring & Symmes, 2006). Whitefly courtship and mating involves different phases including initial contact, parallel orientation, male antennal drumming, male abdominal undulation, wing flicking, bumping or pushing and copulation (Las, 1980). Kanmiya (1996) suggested that prolonged courtship behaviour is due to the necessity for sexual stimulation in the female that is achieved by repeated emission of the male acoustic signals as well as persistent wing flicking. Acoustic signals produced during mating and mate-finding are considered to be features of the specific mate-recognition system (Kanmiya, 1996). Sounds are produced by contractions of the whitefly thoracic muscles that make the abdomen move up and down without wing movement. Male *T. vaporariorum* produce intervals of vibratory sounds composed of a sequence of ‘chirps’. Female response sounds have been recognized. Males and female apparently exchange signals throughout the sequence of mate finding and mating.

Trialeurodes vaporariorum oviposition has been divided into three stages: a pre-oviposition period, a maturation period and mature period. Most mating occurs in the first day after adult emergence and both males and females mate multiple times in their lifetime (Perring & Symmes, 2006). Pre-oviposition on tomato lasted approximately 1.3 days and was followed by the maturation period during which the oviposition rate increases until the mature period where oviposition is relatively constant (called the daily oviposition capacity) (van Lenteren & Noldus, 1990).

1.2 Whitefly Behavioural Manipulation

The objective of insect behavioural manipulation is to prevent a pest from finding and/or damaging a crop or resource of interest by disrupting a pest's host searching strategies (Foster & Harris, 1997). Although many actions associated with controlling pests (e.g. spraying pesticides, crop rotation) can result in intentional or unintentional changes in insect behaviour, the terminology – behaviour manipulation – is often used to describe the use of stimuli (chemical or visual) that induce changes in insect response. Methods of modifying insect behaviour are classified into two groups based on how they act over long-distances (host finding) versus short-distances (host acceptance). Factors of insect spatial dynamics that may be manipulated include insect colonization patterns, insect movement speed and sensory modes of host plant location (Potting *et al.*, 2005).

1.2.1 Whitefly host plant selection

As generalists insects that feed and colonize plants from many different families, *T. vaporariorum* must detect and respond to a complex array of cues that are activated over long and short-distances to select suitable feeding and oviposition sites (Thorsteinson, 1960; Foster & Harris, 1997). In the subsequent sections, I have divided whitefly host selection into three categories including responses to (1) long-distance cues (no direct contact with plant or source material), (2) short-distance external cues (direct contact with source material or external leaf parts), and (3) short-distance internal cues (direct contact with internal leaf parts). For each category of host selection, the main sensory modes of host detection (visual, chemoreception [olfaction and gustation] and mechanoreception) used by *T. vaporariorum* and *B. tabaci* are described.

1.2.1.1 Long-distance host finding (no direct contact)

Most research has indicated that *T. vaporariorum* responses to long-distance cues are mediated largely by adult responses to visual stimuli (Lloyd, 1922; Vaishampayan *et al.*, 1975; Coombe, 1981; Gillespie & Quiring, 1987; Gillespie & Quiring, 1992). Research has shown *T. vaporariorum* are attracted to transmitted/reflected light in the green-yellow (520-590 nm) and ultra-violet (280-380 nm) regions of the spectrum and are inhibited by light in the blue-violet (400 nm) and red (610-700 nm) regions of the spectrum (Vaishampayan *et al.*, 1975; Coombe, 1981; Gillespie & Quiring, 1992; Mellor *et al.*, 1997). As far as is known, whiteflies possess divided compound eyes with separate dorsal and ventral regions (Mellor *et al.*, 1997). For *B. tabaci,* it has been speculated that the larger ventral region of the eye responds primarily to yellow light whereas the smaller dorsal region responds to UV light (Mound, 1962). Mound hypothesized that UV light provides a stimulus for migratory behaviour (UV represents the sky on a sunny day) and suggested that yellow light induces host-finding behaviour (the leaves of most green-leaved plants have a maximum reflection between 500 and 600 nm). Regional specialization of whitefly eyes has been supported by work done with yellow sticky traps. Researchers found that placing a yellow card below a whitefly evoked cessation of wing movement and a ‘fall reflex’ whereas when the yellow trap was placed above or in front of the whitefly no response occurred (Gerling, 1990; Gillespie & Quiring, 1992; Mellor *et al.*, 1997).

1.2.1.2 Short-distance host evaluation and acceptance

While most research indicates that long-distance host finding is based on visual cues, the key drivers to short-distance selection appear to be multisensory. Structural analysis of whitefly antennae found that *T. vaporariorum* possess antennal sensilla that enable it to detect mechanical, olfactory, temperature and humidity cues within its environment (Mellor & Anderson, 1995a; b). Although whitefly antennae possess olfactory sensilla, the role of olfaction in whitefly host plant selection remains unclear. Results from previous whitefly studies suggest that long-distance olfactory responses are not involved with orientation towards a plant before landing (Mound, 1962; Noldus *et al.*, 1986c). However, it seems likely that some olfaction plays a role in detecting probably hosts at close range, i.e., < 1m. Research done in a Y-tube olfactometer demonstrated that whiteflies were attracted to their host-plant odours (Vaishampayan *et al.*, 1975). Furthermore, male olfactory responses to female sexual pheromones were found for *T. vaporariorum* (Li & Maschwitz, 1985). Males were attracted to females within a close range (1 – 2 cm) and arrested by the close proximity of the females. Work done with *B. tabaci* using a vertical olfactometer demonstrated a repellency of ginger oil over a small distance of 1-2 mm (Zhang *et al.*, 2004).

The first physical contact between a whitefly and a plant occurs after a whitefly lands on the leaf surface. Once on a plant, whiteflies walk to the leaf undersides and begin probing the leaf tissue just below the epidermis (van Lenteren & Noldus, 1990). Similar to thrips and leafhoppers, whiteflies have sensory structures on the tips of their labium that may provide chemosensory and mechanosensory functions of host selection (Walker & Gordh, 1989; Hunter *et al.*, 1996). Shallow probing suggests that whiteflies, like aphids, recognize potential hosts by tasting leaf tissues before reaching the plant phloem (Vanvianen *et al.*, 1988). Gustation, by definition, is based on tactile, contact chemoreception (Thorsteinson, 1960).

Whitefly response to chemicals in the plant epidermis and/or mesophyll layers appears to be the main determinant for host acceptance (Molyneux *et al.*, 1990; Lei *et al.*, 1999). While the search for specific factors that affect whitefly preference has been explored by various authors, it is not currently known which plant chemicals have the greatest influence on whitefly host acceptance or rejection (Costa *et al.*, 1991a). If, after short probes, a whitefly deems a plant acceptable the stylet penetrates intercellularly through successive leaf tissue layers. When the phloem sieve element is reached, phloem feeding begins (Figure 1.2) (Freeman *et al.*, 2001). After locating a phloem sieve element in an acceptable plant, a whitefly will feed continuously from the one site where it extracts phloem while keeping the plant cells alive (Thompson & Goggin, 2006).

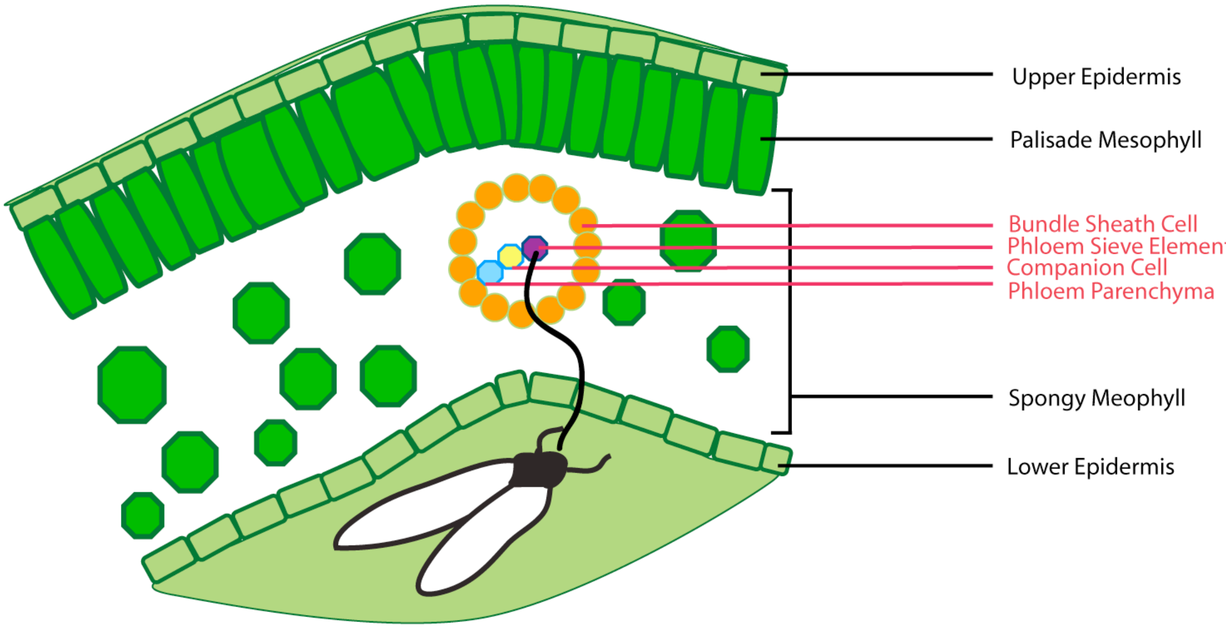

Figure 1.2. Leaf cross section showing location of whitefly feeding in the phloem sieve elements.

Generally, whiteflies are considered to be non-destructive feeders because their piercing/sucking mode of feeding causes less tissue damage to plants than chewing insects. It is thought that by probing leaf cells intercellularly, whiteflies avoid compartmentalized allelochemicals that might otherwise be toxic. *Bemisia tabaci* mouthparts are made up of a maxillary stylet which includes a labrum (the upper lip), a labium (lower lip) and a stylet (Freeman *et al.*, 2001). The stylets of young *T. vaporariorum* nymphs and adults are approximately 120 μm and 200 μm long respectively (Vanderkamp & van Lenteren, 1981). The labium is made up of four segments. The tip of the labium is anchored to the leaf surface using salivary material prior to stylet penetration. When an adult whitefly is not feeding, the stylet bundles are contained within the labium. For young whiteflies, mobile first instar nymphs establish feeding sites that are used by all subsequent instars. Prior to molting, stylets are retracted and no feeding occurs. Freshly molted whiteflies will reinsert their stylets into previously established feeding sites.

Phloem acceptance is defined as continuous phloem feeding that involves simultaneous honeydew excretion (~15 minutes of sustained ingestion) (Lei *et al.*, 1998). Phloem is rich in carbohydrates, amino acids, minerals and soluble nitrogen (Will & van Bel, 2006). Newly developing plant tissues, high in nitrogen, are associated with more nitrogen-based allelochemicals (like alkaloids, cyanogenic glycosides, glucosinolates, proteins, peptides and nonprotein amino acids). The transport of allelochemicals via phloem could potentially play a role in the ecology of host plant resistance against sap sucking insects. However, this has not yet been demonstrated for whiteflies (Molyneux *et al.*, 1990).

1.2.2 Whitefly host preference and performance

Like most polyphagous insects, *T. vaporariorum* demonstrate distinct preferences and performances between plant species and cultivars (Vanderkamp & van Lenteren, 1981). Insect preference refers to behaviour towards part of an individual plant, a particular species or cultivar of plant or a specified set of plant species. It is defined as a deviation from random behaviour and is measured as the relative likelihood of accepting plants that are encountered (Powell *et al.*, 2006). Insect performance is used to describe growth rates, fertilities and fecundities on different host plants. Experimental data provide measurements of insect acceptance and suitability, from which estimates of preference and performance can be made. Acceptability describes the likelihood that a plant will be accepted if encountered by an insect. Suitability has been defined as the various aspects of a host plant that affect the performance of an insect utilizing that plant as food (Singer, 1986).

Although *T. vaporariorum* is polyphagous, it does not eat or oviposit on every plant it encounters. Plants in the Cruciferae, Leguminosae, Malvaceae and Solanacace families are commonly colonized and attacked. However, its host range is not limited to these families (Mound & Halsey, 1978; Byrne & Bellows, 1991). Established hierarchies of *T. vaporariorum* plant preference have been described by some as follows: eggplant > gherkin > cucumber > gerbera > melon > tomato > sweet pepper (van Lenteren &

Noldus, 1990; Lei *et al.*, 2001). On preferred hosts, *T. vaporariorum* shows very little movement following initial probing and feeding site establishment. On less preferred hosts *T. vaporariorum* demonstrates increased movement on and away from the leaf, in addition to less feeding (van Lenteren & Noldus, 1990; Lei *et al.*, 1998). Although less preferred plants (e.g. sweet peppers) are considered to be poor host plants, in the absence of other plants, whitefly populations can still reach high levels.

In natural systems, a reduction in the number and complexity of cues used in food choice is thought to clarify the differences between foods and nonfoods for generalist insects (Bernays, 1996). The ability of insects to learn visual or olfactory cues associated with preferred host plants can reduce searching times for food and thereby increase survival (Turlings *et al.*, 1993; Potting *et al.*, 2005). For many animals, when more attention is paid to the inputs of one sense (e.g. vision), subsequently less attention is paid to cues associated with other senses (e.g. olfaction) (Roitblat, 1987).

The optimum oviposition theory, also known as the preference-performance hypothesis, predicts when immature insects are not involved with host plant selection, females should choose oviposition sites conducive to optimum offspring survival (Jaenike, 1978; Thompson, 1988). Adult whiteflies tend to feed and oviposit on the same leaves (van Lenteren & Noldus, 1990). Whitefly nymphs (stages 2 to 4) are sessile and unable to escape predation or move to alternate host plants. Therefore, it is the ovipositing females that are responsible for selecting the developmental location and food source of their offspring. A gravid female is expected to lay her eggs on leaves that will remain in good condition the longest and, by doing, provides her offspring with a suitable food source for as long as possible (Noldus *et al.*, 1986c).

For whitefly species, the preference-performance relationship appears to depend upon which species and plant is being investigated. Experiments done with *B. tabaci* found females were not able to respond to host plant quality with respect to finding the best host for offspring survival (Costa *et al.*, 1991b). This work differs from results with *T. vaporariorum* which found that on preferred plants, *T. vaporariorum* show higher oviposition rates, shorter development times, higher female longevity and lower mortality (van Lenteren & Noldus, 1990).

1.2.3 Factors affecting whitefly behaviour

Whitefly behaviour is affected by intrinsic factors such as insect physiology, state and previous experiences, and by extrinsic factors, such as abiotic conditions and biotic factors (Bird & Kruger, 2006). In the following tables, I have reviewed key research papers that have evaluated these factors (Tables 1.1–1.5). A few whitefly species, which are pests, have received extensive coverage in the scientific literature. However, behaviour terminology tends to be inconsistent and, at times, inappropriately used. Therefore, I grouped factors affecting whitefly behaviour applying the same categories that I used to describe whitefly host selection (long-distance cues, short-distance cues [external to leaf], and short-distance cues [internal to the leaf]). For each factor, I list which whitefly species was tested (*B. tabaci* or *T. vaporariorum*) and suggest which whitefly senses may be involved (vision, chemoreception [olfaction and gustation] and mechanoreception). Furthermore, I have attempted to classify whitefly responses to factors using six key terms (attraction, repellence, arrestment, deterrence, stimulant and acceptance) (Pluthero & Singh, 1984; Jackson *et al.*, 2000; Koul, 2005; Mauchline *et al.*, 2005; Schuster *et al.*, 2009). For each whitefly response, I have further defined specific behaviours (movement, settling, feeding, or oviposition) that may occur during that response.

Table 1.1. Definitions of terminology used to categorize factors that affect whitefly responses, senses and behaviours according to insect distance from the source.

Distance from Source	Whitefly Response	Whitefly Senses	Whitefly Behaviours
Long-Distance	Attraction	Vision Olfaction	**Movement:** oriented flight towards **Settling:** landing, rate of arrival
	Repellence	Vision Olfaction	**Movement:** oriented flight away **Settling**: avoidance, aversion
Long & Short-Distance	Arrestment	Vision Olfaction Gustation Mechanoreception	**Settling**: increased settling, aggregation
Short-Distance	Deterrence	Vision Olfaction Gustation Mechanoreception	**Movement**: increased departure, latency **Settling**: antisettling, decreased settling **Feeding**: inhibits feeding
	Stimulation	Gustation Mechanoreception	**Feeding**: elicits feeding
	Acceptance	Gustation	**Feeding**: sustained feeding **Oviposition**: eggs deposited

Table 1.2. Internal factors that affect whitefly behaviour.

Internal Factors		Whitefly Species	Whitefly Behaviour	Sources
State and Physiology	Egg load	*B. tabaci*	Movement Settling Feeding Oviposition	(Veenstra & Byrne, 1998; Blackmer & Byrne, 1999)
	Age	*T. vaporariorum*	Movement Settling Feeding Oviposition	(Noldus *et al.*, 1985; Noldus *et al.*, 1986b)
	Time since last feeding bout		Movement Settling Feeding Oviposition	
	Sex	*B. tabaci*	Movement Settling Feeding Oviposition	(Blackmer & Byrne, 1993)
Previous Experience	Host plant	*B. tabaci* *T. vaporariorum*	Movement Settling Feeding Oviposition	(Noldus *et al.*, 1986b; Lei *et al.*, 1998; Veenstra & Byrne, 1998)
	Natural enemies	*B. tabaci*	Movement Settling Feeding Oviposition	(Nomikou *et al.*, 2003; Meng *et al.*, 2006)

Table 1.3. Long-distance factors that affect whitefly behaviour.

Biotic and Abiotic Factors		Whitefly Species	Whitefly Senses	Whitefly Response	Whitefly Behaviour	Sources
Plant Traits	Colour	*B. tabaci* *T. vaporariorum*	Vision	Attraction	Movement Settling	(Lloyd, 1922; Mound, 1962; Vaishampayan *et al.*, 1975; Coombe, 1981)
	Shape	*T. vaporariorum*	Vision	No effect		(van Lenteren & Noldus, 1990)
	Plant volatiles	*T. vaporariorum*	Olfaction	Attraction Repellence	Movement Settling	(Vaishampayan *et al.*, 1975)
		T. vaporariorum	Olfaction	No effect		(van Lenteren & Noldus, 1990)
Community	Plant diversity	*B. tabaci*	Vision Olfaction	Attraction Repellence Arrestment	Movement Settling	(Bernays, 1999) (Bird & Kruger, 2006)
	Conspecifics	*B. tabaci* *T. vaporariorum*	Vision Olfaction	Attraction Repellence Arrestment	Movement Settling	
	Natural Enemies	*B. tabaci*	Vision Olfaction	Attraction Repellence Arrestment	Movement Settling	(Nomikou *et al.*, 2003; Meng *et al.*, 2006)
Climate	Temperature	*B. tabaci* *T. vaporariorum*			Movement Settling	(Blackmer & Byrne, 1993; Riis & Nachman, 2006)
	Humidity	*B. tabaci*			Movement Settling	(Berlinger, 1986; Blackmer & Byrne, 1993)
	Light	*B. tabaci* *T. vaporariorum*			Movement Settling	(van Lenteren & Noldus, 1990; Doukas & Payne, 2007)
	CO_2	*B. tabaci*			Settling	(Butler *et al.*, 1986; Tripp *et al.*, 1992)
	Wind speed	*B. tabaci*			Movement Settling	(Blackmer & Byrne, 1993; Isaacs *et al.*, 1999b)
Other	Greenhouse size	*T. vaporariorum*		Attraction Repellence	Movement Settling	(Noldus *et al.*, 1986a)
	Reflective mulches		Vision	Attraction Repellence	Movement Settling	(Smith *et al.*, 2000)
	Light-Emitting Diodes	*B. tabaci*	Vision	Attraction Repellence	Movement Settling	(Chu *et al.*, 2003)
	UV-Blocking Films	*T. vaporariorum*	Vision	Attraction Repellence	Movement Settling	(Doukas & Payne, 2007)
	Trap Shapes	*T. vaporariorum*	Vision	Attraction Repellence	Movement Settling	(Mainali & Lim, 2008)

Table 1.4. Short-distance external to leaf factors that affect whitefly behaviour.

Biotic and Abiotic Factors		Whitefly Species	Whitefly Sense	Whitefly Response	Whitefly Behaviour	Sources
Plant Traits	Leaf colour	*B. tabaci* *T. vaporariorum*	Vision	Arrestment Stimulant	Movement Settling	(van Lenteren & Noldus, 1990)
	Leaf shape	*T. vaporariorum*	Vision	No effect		(van Lenteren & Noldus, 1990)
	Leaf size	*B. tabaci*	Vision Mechanoreception	Arrestment Deterrence Stimulant	Movement Settling	(Ohnesorge, 1981)
	Leaf age	*B. tabaci* *T. vaporariorum*	Vision Olfaction Mechanoreception	Arrestment Deterrence Stimulant	Movement Settling	(Ohnesorge, 1981; Noldus *et al.*, 1986b)
	Leaf trichomes	*B. tabaci* *T. vaporariorum*	Vision Olfaction Mechanoreception	Arrestment Deterrence Stimulant	Movement Settling	(Vanderkamp & van Lenteren, 1981; Vanvianen *et al.*, 1988; Neal & Bentz, 1999)
	Leaf cuticle	*T. vaporariorum*	Vision Olfaction Mechanoreception	Arrestment Deterrence Stimulant		(Vanderkamp & van Lenteren, 1981; Leite *et al.*, 2006)
	Leaf veins	*B. tabaci* *T. vaporariorum*	Vision Mechanoreception	Arrestment Deterrence Stimulant		(Vanvianen *et al.*, 1988; Inbar *et al.*, 1999)
	Plant species	*B. tabaci* *T. vaporariorum*	Vision Olfaction Mechanoreception	Arrestment Deterrence Stimulant		(van Lenteren & Noldus, 1990)
	Plant architecture	*B. tabaci* *T. vaporariorum*	Vision Mechanoreception	Arrestment Deterrence Stimulant		van Lenteren & Noldus, 1990)
	Plant chemistry	*B. tabaci* *T. vaporariorum*	Olfaction	Arrestment Deterrence Stimulant		(Vaishampayan *et al.*, 1975)
Community	Plant diversity	*B. tabaci*	Vision Olfaction	Arrestment Deterrence Stimulant		(Bernays, 1999)
	Conspecifics	*B. tabaci* *T. vaporariorum*	Vision Olfaction Mechanoreception	Arrestment Deterrence Stimulant		(Blackmer & Byrne, 1999)
	Natural Enemies	*B. tabaci*	Vision Olfaction Mechanoreception	Arrestment Deterrence Stimulant		(Ohnesorge, 1981; Nomikou *et al.*, 2005)
Climate	Temp		Mechanoreception			(Jauset *et al.*, 1998)
	Humidity	*T. vaporariorum*	Mechanoreception			(Mele *et al.*, 1992)
	Light	*T. vaporariorum*	Vision			(Vaishampayan *et al.*, 1975; Coombe, 1982; Jauset *et al.*, 1998)
	Gravity	*B. tabaci*	Mechanoreception		Movement Settling	(Simmons, 1994)
Other	Pesticides	*B. tabaci*	Olfaction Mechanoreception	Arrestment Deterrence		(Liang & Liu, 2002)

Table 1.5. Short-distance internal to leaf factors that affect whitefly behaviour.

Biotic and Abiotic Factors		Whitefly Species	Whitefly Sense	Whitefly Response	Whitefly Behaviour	Sources
Plant Chemistry	Secondary plant components	*B. tabaci* *T. vaporariorum*	Gustation Mechanoreception	Arrestment Deterrence Stimulant Acceptance	Settling Feeding Oviposition	(Vanderkamp & van Lenteren, 1981; Noldus *et al.*, 1986c)
	pH		Gustation	Arrestment Deterrence Stimulant Acceptance	Settling Feeding Oviposition	(Berlinger *et al.*, 1983)
	Amino acids	*B. tabaci*	Gustation	Arrestment Deterrence Stimulant Acceptance	Settling Feeding Oviposition	(Blackmer & Byrne, 1999)
	Carbohydrates		Gustation	Arrestment Deterrence Stimulant Acceptance	Settling Feeding Oviposition	
Fertilizers	Nitrogen	*B. tabaci* *T. vaporariorum*	Gustation	Arrestment Deterrence Stimulant Acceptance	Settling Feeding Oviposition	(Mattson, 1980; Bentz *et al.*, 1996; Blackmer & Byrne, 1999; Jauset *et al.*, 2000)
Plant	Virus		Gustation	Arrestment Deterrence Stimulant Acceptance	Settling Feeding Oviposition	
	Water Stress	*B. tabaci*	Gustation	Arrestment Deterrence Stimulant Acceptance	Settling Feeding Oviposition	(Isaacs *et al.*, 1998; Inbar *et al.*, 2001)
	Mechanical damage	*B. tabaci*	Gustation	Arrestment Deterrence Stimulant Acceptance	Settling Feeding Oviposition	(Inbar *et al.*, 2001)
Other	Imidacloprid (systemic)	*B. tabaci*	Gustation	Arrestment Deterrence Stimulant Acceptance	Settling Feeding Oviposition	(Isaacs *et al.*, 1999a)

1.3 Pest Management Tactics that Manipulate Whitefly Behaviour

Behaviour manipulation of pests is based on the knowledge that specific cues can trigger predictable and innate actions for insects based on their sensory abilities. Both conventional and alternative pest management techniques are often employed without clear knowledge of how tactics affect insect behaviour. The following section provides background information on the main alternative pest management tactics evaluated in this project and reviews previous work done with *B. tabaci* and *T. vaporariorum*.

1.3.1 Yellow sticky traps

Whitefly attraction to visual cues was detected early in the 20th century and led to the development of pest management techniques such as yellow sticky traps and UV-absorbing films or nets (Lloyd, 1922; Coombe, 1981; Gillespie & Quiring, 1987; Gillespie & Quiring, 1992; Antignus *et al.*, 2001). For *T. vaporariorum*, yellow traps reflecting and transmitting light maximally between 520 nm and 550 nm, and placed at the top of plants, are considered the most effective (Ekbom & Rumei, 1990). Whitefly economic pests such as *B. tabaci* and *T. vaporariorum* are reported to exhibit varying responses to yellow traps depending a number of factors (Gu *et al.*, 2008). Here, the main factors thought to affect whitefly responses to traps were summarized as variations in whitefly species flight behaviours between and within plant rows, colour of trap, height of trap, stickiness of sticky materials, growing conditions (e.g. temperature and lighting), locations of traps within greenhouses, crop growth stage, whitefly density and/or species-specific orientation to the yellow traps (Gu *et al.* 2008 and references therein). Gu *et al.* (2008) found that combinations of yellow sticky traps with parasitoids provided better control of *B. tabaci* within tomato greenhouses than the use of either treatment alone.

1.3.2 Reduced-risk sprays

Reduced-risk sprays (RRSs) are exemplified by insecticidal soaps, vegetable and paraffin oils and plant extracts that have reduced health and environmental impacts compared to synthetic insecticides. These tactics offer simple and effective means of reducing pest populations and many have been shown to have a reduced effect on biological controls (Liu & Stansly, 1995b; Liang & Liu, 2002; Simmonds *et al.*, 2002). Despite ample evidence supporting reduced-risk sprays, commercial adoption is low. A lack of implementation has been attributed to regulatory barriers, high costs, inconsistent responses, the absence of large-scale commercial application, public demand for unblemished plant products and the need for additional research (Isman, 2006).

A number of reduced-risk sprays have been evaluated in both laboratory and greenhouse experiments for *T. vaporariorum* and *B. tabaci* (Table 1.6). The use of these products has been recommended as a means to force whiteflies to oviposit in less preferred locations on the plant (Liu and Stansly 1995). However, whitefly behavioural responses to long- and short-distance cues have not been fully explored and the effects of behaviour modifying materials appears to vary depending upon whitefly species, host plants, experimental setups, methods of application, and spatial scale (Zhang *et al.*, 2004; Liang *et al.*, 2007).

1.3.3 Trap crops

Understanding insect responses to vegetational diversity has received attention since the 1960’s when a general trend for decreased pest pressure in polycultures compared to monocultures emerged (Agrawal *et al.*, 2006). Trap cropping is a method of crop diversification that has a long history of use in traditional farming practices. Trap crops are defined as ‘plant stands that are, *per se* or via manipulation deployed to attract, divert, intercept, and/or retain targeted insects or the pathogens they vector in order to decrease damage to main crops’ (Shelton & Badenes-Perez, 2006). Alternatively, trap crops can be used as monitoring tools or they may function as banker plants that help build up natural enemy populations (Stacey, 1977; Hokkanen, 1991; Pickett *et al.*, 2004; Buitenhuis & Shipp, 2006).

Trap cropping is a form of cultural pest control that has received increased interest in recent years due to problems associated with chemical pesticides. In general, insects amendable to trap crop management are those that demonstrate a preference between host plants, use visual cues to find their hosts and have the ability to make direct and oriented flights (Hokkanen, 1991; Potting *et al.*, 2005). General trap crop guidelines recommend that 10% of the total crop area contain trap crops (Shelton & Badenes-Perez, 2006). Trap crops can be different plant species than the main crop or the same species or cultivar as the main crop but grown at different times in the season. Growers manipulate trap crops and main crops in time and space so that the attractive trap crops are available at critical times of the growing season. Greenhouses have been suggested as ideal sites for trap crop application because of their closed structures, controllable environments and somewhat predicable pest outbreaks (Buitenhuis & Shipp, 2006).

The majority of published research evaluating trap crops for whiteflies has focused on *B. tabaci* rather than *T. vaporariorum* (Table 1.7). In general, results have varied between whitefly biotypes, cropping systems (many experiments were done in a field setting), main crops and trap crops selected. Some authors found that trap crops can reduce or repel whiteflies at certain times in the growing season, while other studies found that some trap crops increased whitefly densities and virus transmission. The most relevant results of trap cropping in greenhouses for *T. vaporariorum* and *B. tabaci* have come from commercial trials with poinsettia crops in Ontario, Canada controls (Murphy *et al.*, 2006). Since 2004, researchers have been combining eggplant (cv. Baby Bell) as a trap crop with biological (Murphy, 2007). These results have demonstrated that healthy eggplants can successfully lure and retain *T. vaporariorum* whiteflies away from poinsettia crops. However, eggplant is not an effective trap for *B. tabaci* (see Table 1.7). Recently, eggplant as a trap crop in poinsettias was tested for both *B. tabaci* and *T. vaporariorum* (Lee *et al.*, 2009). These authors found that an unexpected factor, whitefly mortality on the main crop, was strongly influencing trap crop efficacy. Similar to Murphy (2007), Lee *et al.* 2009 found that eggplants were not attractive to *B. tabaci* whereas these putative trap crops were attractive to *T. vaporariorum*.

Greenhouse growers are particularly interested in quantifying the levels of control achieved with trap crops and in identifying trap plants other than eggplant that could be used (British Columbia Greenhouse Growers Association, personal communication). Eggplant is a slow growing plant that tends to be a good host for many other greenhouse pests and there have been some reports of eggplant becoming a source of pests rather than a sink. Using trap crop plant species from a different plant family than the main crop has been recommended as a means of preventing virus transmission between trap crops and main crops (Hooks & Fereres, 2006).

1.3.4 Plant resistance

Plant resistance to insects has long been considered one of the most potent, economical and effective methods of pest control for agricultural crops (De Ponti *et al.*, 1990). Plant resistance is a relative term. It is defined as any reduction in population growth of a target insect, as influenced by heritable traits of the host plant, compared to a standard variety (De Ponti *et al.*, 1990). Plant resistance to insects is classified into three functional categories: antixenosis, antibiosis and tolerance (Smith, 1989; Cook *et al.*, 2007). Antixenosis are plant traits that reduce insect establishment by changing insect preference behaviours where preference is measured by the number of insects landing and settling on plants. Antibiosis evaluates the effects of resistant plants on insect biology (fecundity, development time, etc). Plant tolerance to insects occurs when genetic qualities of the plant enable it to recover or withstand insect damage.

To evaluate plant resistance to whiteflies, researchers have studied whitefly host-plant attraction (settling), oviposition, adult mortality, and offspring development. Plant resistance to whiteflies has been demonstrated for some whitefly species, under certain experimental methods and against some crops cultivars (Table 1.8).

Table 1.6. Studies evaluating reduced-risk sprays against whiteflies.

Test Material	Host Plant	Whitefly Species	Results	Source
Ajuga reptans	Tobacco	*T. vaporariorum*	Extract acts as ecdysteroids. More effective on eggs than on nymphs.	(Mele *et al.*, 1992)
Chenopodium ambrosioides **Neem extract**		*T. vaporariorum*	*Chenopodium* extracts were more effective than neem but was toxic to *E. formosa*.	(Chiasson *et al.*, 2004)
Garlic extract **Insecticidal soap** **Mineral Oil** ***Nicotiana gossei***	Tomato	*B. tabaci*	Mineral oil was as effective as the synthetic. Garlic was not effective. Insecticidal soap and *N. gossei* were intermediate.	(Liu & Stansly, 1995b)
Ginger Oil	Tomato	*B. tabaci*	Ginger has some potential but issues of phytotoxicity and coverage.	(Zhang *et al.*, 2004)
Kaolin **Mineral oil**	Melon	*B. tabaci*	Both were deterrent to adult whiteflies.	(Liang & Liu, 2002)
Mineral oil	Chrysanthemum	*T. vaporariorum*	Oil deterred whiteflies for 11 days and was toxic to nymphs.	(Larew & Locke, 1990)
Mineral oil	Collard	*B. tabaci*	Treated nymphs, pupae and crawlers were all affect by oils.	(Sieburth *et al.*, 1998)
Mint family		*B. tabaci*	Essential oil vapors were toxic to adults	(Calmasur *et al.*, 2006)
Neem extract	Poinsettia	*B. tabaci*	Neem reduced nymphs only.	(Price & Schuster, 1991)
Neem extracts **Pyrethrum** **Naphthoquinones**	Tobacco	*T. vaporariorum*	Neem offered the most potential for biological control programs.	(Simmonds *et al.*, 2002)
Neem extracts	Cucumber	*B. tabaci*	Neem reduced settling	(Wen *et al.*, 2009)
Nicotiana gossei	Tomato	*B. tabaci*	Effective at controlling all life stages including eggs.	(McKenzie *et al.*, 2005)
Nicotiana gossei	Tomato	*T. vaporariorum*	Topical application to nymphs caused mortality	
Pongam Oil	Chrysanthemum	*T. vaporariorum*	Pongam was an effective long-lasting adult deterrent.	(Pavela & Herda, 2007)
15 Detergents **2 Oils** **1 Soap**	Zucchini Tomato Poinsettia	*B. tabaci*	Many soaps and detergents can deter and effectively control whiteflies.	(Butler *et al.*, 1993)
22 commercial products and 42 other products	Tomato	*B. tabaci*	Ultra-Fine Oil and olive oil reduced oviposition and transmission of TYLCV in screenhouse trials.	(Schuster *et al.*, 2009)
53 essential oils	Tomato	*T. vaporariorum*	Bay, caraway seed, clove, eucalyptus, pennyroyal, peppermint, rosewood, spearmint & tea tree oils were effective against adults, nymphs & eggs.	(Choi *et al.*, 2003)

Table 1.7. Studies reporting trap crops evaluated for whiteflies.

Trap Crop	Main Crop	Whitefly Species	Results	Sources
Cantaloupe	Cotton	*B. tabaci*	Densities somewhat reduced but not below economic thresholds	(Castle, 2006)
Cabbage **Cilantro** **Corn** **Roselle** **Velvetbean**	Bean	*B. tabaci* *T. vaporariorum*	No effect of trap crops on main crop densities	(Smith *et al.*, 2001)
Corn **Eggplant**	Bean	*B. tabaci*	No effect of trap crops.	(Smith & McSorley, 2000)
Cover crops: **Peanuts** **Coriander**	Tomatoes	*B. tabaci*	Results varied but tomatoes with cover crops had equal or better yields.	(Hilje *et al.*, 2001)
Corn **Cucumber** **Eggplant**	Tomato	*B. tabaci*	Cucumber decreased the incidence of TYLCV on tomatoes.	(Al-Musa, 1982)
Eggplant **Tomato**	Tomato	*B. tabaci*	Eggplant and tomato treated with imidacloprid reduced whiteflies on neighboring tomatoes.	(Stansly *et al.*, 1998)
Eggplant	Poinsettia	*B. tabaci* *T. vaporariorum*	Eggplant works as a trap crop for *T. vaporariorum* but not for *B. tabaci.*	(Murphy, 2006)
Eggplant	Poinsettia	*B. tabaci* *T. vaporariorum*	Eggplant was more attractive to *T. vaporariorum* than *B. tabaci.*	(Lee *et al.*, 2009)
Groundcherry	Cotton	*B. tabaci*	Groundcherry treated with pesticides reduced densities on cotton. Untreated trap crops increased densities on cotton.	(Ellsworth *et al.*, 1992)
Squash	Tomato	*B. tabaci*	Squash reduced densities and TYLC on tomatoes.	(Schuster, 2004)

Table 1.8. Studies reporting plant resistance against whiteflies.

Host Plant	Whitefly Species	Mode of Resistance Evaluated	Sources
Alfalfa	*B. tabaci*	Antibiosis and antixenosis	(Jiang & Walker, 2007)
Brassica crops	*Aleyrodes proletella*	Antibiosis and antixenosis	(Nebreda *et al.*, 2005)
Broccoli	*B. tabaci*	Antixenosis	(Cohen *et al.*, 1996)
Cabbage	*B. tabaci*	Antibiosis	(An *et al.*, 2007)
Cabbage	*B. tabaci*	Antibiosis	(Zang *et al.*, 2006)
Cantaloupe	*B. tabaci*	Antibiosis and antixenosis	(Costa *et al.*, 1991b)
Cantaloupe	*B. tabaci*	Antibiosis	(Nava-Camberos *et al.*, 2001)
Cantaloupe	*B. tabaci*	Antixenosis	(Cohen *et al.*, 1996)
Cole crops	*B. tabaci*	Antibiosis and antixenosis	(Jackson *et al.*, 2000)
Cotton	*B. tabaci*	Antibiosis and antixenosis	(Walker & Natwick, 2006)
Cotton	*B. tabaci*	Antibiosis and antixenosis	(Costa *et al.*, 1991b)
Cotton	*B. tabaci*	Antibiosis	(Nava-Camberos *et al.*, 2001)
Cotton	*B. tabaci*	Antibiosis	(Zang *et al.*, 2006)
Cotton	*B. tabaci*	Antixenosis	(Cohen *et al.*, 1996)
Eggplant	*B. tabaci*	Antixenosis	(Leite *et al.*, 2002)
Hibiscus	*B. tabaci*	Antixenosis	(Cohen *et al.*, 1996)
Kidney bean	*B. tabaci*	Antibiosis	(Zang *et al.*, 2006)
Lantana	*B. tabaci*	Antixenosis	(Cohen *et al.*, 1996)
Lettuce	*B. tabaci*	Antixenosis	(Cohen *et al.*, 1996)
Lettuce	*B. tabaci*	Antibiosis and antixenosis	(Costa *et al.*, 1991b)
Pumpkin	*B. tabaci*	Antibiosis and antixenosis	(Costa *et al.*, 1991b)
Squash	*B. tabaci*	Antibiosis	(Zang *et al.*, 2006)
Sweet Pepper	*B. tabaci*	Antibiosis	(Nava-Camberos *et al.*, 2001)
Sweet pepper	*T. vaporariorum*	Antibiosis and antixenosis	(Laska *et al.*, 1982)
Sweet Pepper	*T. vaporariorum*	Antibiosis and antixenosis	(van Lenteren *et al.*, 1989)
Sweet pepper	*T. vaporariorum*	Antixenosis	(Lei *et al.*, 1999)
Tobacco	*B. tabaci*	Antibiosis	(Zang *et al.*, 2006)
Tomato	*B. tabaci*	Antixenosis	(Sanchez-Pena *et al.*, 2006)
Tomato	*B. tabaci*	Antibiosis and antixenosis	(Costa *et al.*, 1991b)
Tomato	*B. tabaci*	Antibiosis	(Liu & Stansly, 1995a)
Tomato	*Both*	Antibiosis and antixenosis	(De Ponti *et al.*, 1990)
Tomato	*T. vaporariorum*	Antibiosis	(De Ponti *et al.*, 1975)
Tomato	*T. vaporariorum*	Antixenosis	(Lei *et al.*, 1999)
White-flowered Gourd	*B. tabaci*	Antibiosis and antixenosis	(Kishaba *et al.*, 1992)
Zucchini	*B. tabaci*	Antibiosis and antixenosis	(Costa *et al.*, 1991b)

1.4 Research Objectives

Trialeurodes vaporariorum is a major agronomic pest in vegetable and ornamental greenhouses. In 2005, both the British Columbia Greenhouse Growers' Association and the Pesticide Risk Reduction Program of Agriculture and Agri-Food Canada (AAFC) defined whiteflies as a priority greenhouse pest (AAFC, 2005). In British Columbia, approximately 100 hectares of greenhouse sweet peppers (*Capsicum annuum*) are grown and whitefly damage is estimated to cost $3 - 4 million/year (British Columbia Greenhouse Growers' Association, personal communication 2007). Whiteflies reduce plant vigor and crop quality by removing phloem, excreting honeydew and by transmitting plant viruses. Biological control programs for whitefly management are commonly used within commercial greenhouses. However, chemical intervention, if required for whitefly control, can lead to the loss of biological control programs that result in financial losses to the grower. The continual development of whitefly resistance to previously effective insecticides has further complicated whitefly management. These issues highlight the need for alternative pest management strategies that complement and enhance currently used biological control programs.

A better understanding of alternative tactics and their resultant effect on whitefly behaviour is essential to attaining reliable results and to increasing grower adoption of these techniques. This project started with the intention to develop a push-pull strategy for *T. vaporariorum* control on sweet peppers. Push-pull is an example of a coordinated management strategy that manipulates insect behaviour for the purpose of pest management (Cook *et al.*, 2007). The strategy uses combinations of repellent and attractive cues to direct the movement of insects away from protected resources. In early experiments (Chapter 3), it became clear that pushing whiteflies using long-distance cues (such as plant extracts) did not greatly influence whitefly settling and oviposition behaviours. Whitefly behaviour was more influenced by short-distance factors. Therefore, the push-pull terminology was discontinued and terminology associated with insect behavioural manipulation was adopted (see Table 1.1 for definitions on whitefly responses, senses and behaviours).

In the following project, a number of alternative whitefly control tactics were evaluated on sweet peppers including yellow sticky traps (YSTs), trap crops (TCs), reduced-risk sprays (RRSs) (e.g. insecticidal soaps and oils, plant extracts) and plant resistance (PR). The use of reduced-risk sprays (RRSs) in this thesis represent alternative plant protectants considered to have reduced health and environmental impacts compared to conventional pesticides (Fraser, 2005). TCs, YSTs, RRSs and PR were selected based on their potential to modify *T. vaporariorum* long- and short-distance behaviours, for their less toxic nature and because they had received some attention in the scientific literature. Furthermore, the application of these methods was considered to be practical for use within commercial greenhouses.

The goal of this research was to gain an understanding of the behavioural response of *T. vaporariorum* to alternative control tactics and to explore how these tactics (TCs, YSTs, RRSs and PR) could be used to improve management in commercial sweet pepper greenhouses. The objective was to identify which tactics had the greatest influence on whitefly settling and oviposition behaviours and to combine these tactics in a whitefly behavioural manipulation strategy. The following research questions provided the framework from which this thesis was developed and conducted:

- Which individual tactics are the greatest modifiers of whitefly long- and short-distance host selection behaviours and which methods are most effective at reducing whitefly populations on sweet peppers?
- Can the control efficacy of individual tactics be improved through combinations with other tactics?

    If so:

    - Which combinations are most effective?

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Chapter 2[*] Greenhouse whitefly (*Trialeurodes vaporariorum)* settling and oviposition on sweet peppers (*Capsicum annuum)* in the presence of trap crops and yellow sticky traps

2.1 Introduction

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae), is a serious pest of vegetable and ornamental greenhouse crops (Oliveira *et al.*, 2001; AAFC, 2005). In commercial sweet pepper (*Capsicum annuum)* greenhouses, whiteflies reduce yields by extracting water, phytosynthates and amino acids from the plant (Lloyd, 1922; Mound & Halsey, 1978). In addition, excreted whitefly honeydew covers leaf foliage, which fosters the growth of sooty mold and reduces photosynthesis (Lloyd, 1922; Buckner *et al.*, 1994; Smith *et al.*, 2001). When honeydew is detected on pepper fruits, growers are confronted with an additional expense of washing peppers prior to shipping. Within British Columbia, Canada, the estimated cost of *T. vaporariorum* damage is $3 – 4 million/year (British Columbia Greenhouse Growers' Association, personal communication). The two main *T. vaporariorum* management tactics used within greenhouses are biological and chemical control. Biological controls, such as *Encarsia formosa* (Gahan), do not always maintain adequate control and chemical pesticides are commonly applied. Chemical spraying for whiteflies or other greenhouse pests can lead to losses of existing biological controls programs and to insecticide resistance. In order to reduce economic losses associated with *T. vaporariorum* damage, commercial growers and the greenhouse industry consider alternative whitefly control tactics a high research priority.

Both trap crops and yellow sticky traps are recommended for monitoring and controlling *T. vaporariorum* within greenhouses (Ferguson *et al.*, 2003). However, there is limited information available regarding the comparative efficacy between these two traps and there is a need for crop-specific study of traps due to the strong influence of host plant on trap efficacy (Muirhead-Thomson, 1991). Insect trapping is based on

[*] A version of this chapter will be submitted for publication. Moreau, T.L. and M.B. Isman. 2010. Whitefly settling and oviposition on sweet peppers in the presence of yellow sticky traps and trap crops.

manipulating particular host selection behaviours. As generalist phloem-feeding insects, *T. vaporariorum* detect and respond to a complex array of cues that stimulate responses over long-distances (finding-type behaviours) or short-distances (acceptance-type behaviours) (Foster & Harris, 1997). Previous studies indicate that *T. vaporariorum* long-distance host finding (no direct contact with plant) is based on responses to visual cues and that short-distance host acceptance (direct contact with plant) happens only after the acquisition of gustatory information obtained from probing leaf surfaces and sampling internal plant chemical cues (Mound, 1962; Vaishampayan *et al.*, 1975a; Vaishampayan *et al.*, 1975b; Vanderkamp & van Lenteren, 1981; Noldus *et al.*, 1986; van Lenteren & Noldus, 1990).

Reports of *T. vaporariorum* visual attraction to coloured cards was published early in the 1920's and led to the widespread use of yellow sticky traps as monitoring tools (Lloyd, 1922; Coombe, 1981; Gillespie & Quiring, 1992; Antignus *et al.*, 2001). Less is known about whitefly olfactory responses. Although *T. vaporariorum* antennae possess olfactory sensilla, the role of olfaction in whitefly host plant finding remains unclear (Mellor & Anderson, 1995b; a). Earlier work suggests long-distance olfactory responses are not involved (Mound, 1962; Noldus *et al.*, 1986). However, it seems likely that some olfaction plays a role in detecting hosts within close ranges, i.e., < 1m.

Trap cropping is a form of intercropping in which a preferred host plant is used to attract and arrest insect pests away from less-preferred host plants. Trap crops may be used as pest-monitoring tools, control tactics or as banker plants (plants that provide alternative food, hosts or shelter for natural enemies) (Stacey, 1977; Hokkanen, 1991; Buitenhuis & Shipp, 2006). Trap crops can be a different species from the main crop (e.g., main crop = pepper, trap crop = eggplant) or the same species or cultivar as the main crop grown at a different time (e.g., main crop = potato, trap crop = early or late potato).

Trialeurodes vaporariorum performance on host plants corresponds to adult preferences (van Lenteren & Noldus, 1990). Rankings of *T. vaporariorum* host preferences, as indicated by the number of whiteflies on a plant in a choice situation, found the most- to less-preferred host species were: eggplant > gherkin > cucumber >

melon > tomato > sweet pepper. Although preferred host plants such as eggplant have been recommended as *T. vaporariorum* trap crops (Ferguson *et al.*, 2003; Lee *et al.*, 2009), the viability and practicality of this tactic for use by sweet pepper growers is uncertain.

Only a few replicated experiments have evaluated trap crop efficacy for *T. vaporariorum* (Smith *et al.*, 2001; Buitenhuis *et al.*, 2007; Lee *et al.*, 2009). At the time of writing, the author identified no specific study of whitefly trap crops with sweet peppers. Evaluations of *T. vaporariorum* trap crops in poinsettia greenhouses indicated that healthy eggplants (c.v., "Baby Bell") combined with biological control programs successfully reduced *T. vaporariorum* on poinsettias (Murphy *et al.*, 2006). However, the influences of the two tactics (trap crops versus biological controls) were not independently evaluated. Recently, Lee *et al.* (2009) found that adult *T. vaporariorum* mortality on poinsettia crops strongly influenced the effectiveness of an eggplant trap crop. Through simulation studies, the authors found low adult mortality on main crops was a requisite for a preferred host plant to function as a trap crop. In particular, patterns of *T. vaporariorum* host adaptation and its effects on preferences were highlighted a factors affecting trap crop outcomes (Lee *et al.* 2009).

In British Columbia (BC), Canada, some greenhouse growers use eggplant as a whitefly trap crop but most growers require more information before adopting new pest management techniques (British Columbia Greenhouse Growers' Association, personal communication). The main interest of BC growers was to quantify *T. vaporariorum* control achieved with eggplant trap crops and to identify alternative trap crop species. Eggplants' ability to support other greenhouse pests (e.g. aphids and thrips) and its slow germination and growth has promoted grower interest in different trap crop species.

In this study, the objective was to investigate whitefly preferences between two trap crop species and yellow sticky traps to determine which trap was most effective at reducing *T. vaporariorum* populations on sweet peppers. As a measure of whitefly behaviour and to estimate trap efficacy, whitefly settling on peppers and traps was compared. More specifically, four questions were asked:

1. Which traps (trap crops or yellow sticky traps) are most effective at preventing dispersing whiteflies from settling and ovipositing on sweet peppers?
2. Can plant species other than eggplant be used as effective whitefly trap crops?
3. Do trap crops and yellow sticky traps increase resident whitefly departure from peppers?
4. Does the presence of trap crops affect total whitefly populations?

2.2 Materials and Methods

2.2.1 Dispersing whitefly response to trap crops and yellow sticky traps

In preliminary greenhouse studies comparing whitefly densities on eleven *T. vaporariorum* host plants, eggplant (c.v., "Dusky", West Coast Seeds) and summer squash (c.v., "Starship", West Coast Seeds) supported the highest densities of adults. In the following, dispersing adult settling and oviposition on pepper plant stands (representing main crops) in the presence of two trap crops (eggplant and squash) and yellow sticky traps (Horiver, Koppert) were compared to a control - no trap (Figure 2.1). Dispersing *T. vaporariorum*, those not present on a plant at the start of the experiment, represented adult whiteflies that would be actively moving and seeking a host plant. Plant stands holding excised sweet pepper leaves, *C. annuum* (c.v., "Forever", Enza Zaden), were developed to mimic whole pepper plants.

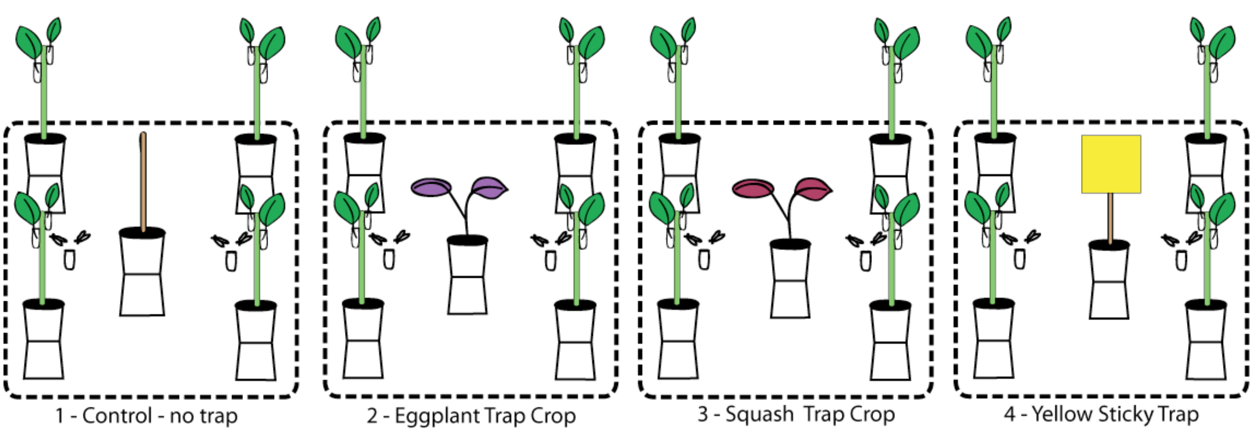

Figure 2.1. ***Trialeurodes vaporariorum*** **cage bioassay (60 adults/cage) comparing settling and oviposition on main crops in four replicated treatments (1) control-no trap, (2) eggplant, (3) summer squash and (4) YSTs.**

Experiments were conducted in BioQuip® Bugdorm-2 cages (60 x 60 x 60 cm) in a windowless University of British Columbia (UBC) laboratory under fluorescent lights from November to December 2008. In each cage, four pepper stands (two leaves/stand) were placed in a square formation (25 cm between plants) and trap treatments were placed in the cage centre. Experimental plant stands consisted of two pepper leaves placed in vials secured to a vertical stand at heights of 30 and 35 cm. Excised leaves were selected from four-month old peppers to ensure that leaf age classes were taken from similar growing points with comparable surface areas. Small leaves were placed in the top vial of the plant stand and larger leaves were placed in the bottom vial. Leaves were immediately placed in water following excision. Eggplant and squash were sown at different times to obtain plants of similar sizes. Eggplants were used at 8 wk and squash at 5 wk. Seedlings were pruned to two leaves/plant immediately before the experiment. Yellow sticky traps were cut to an area of 100 cm^2 and secured to a stand. Unlike eggplant and squash treatments, adults on the yellow sticky traps were unable to leave the trap once they landed. Natural populations of *T. vaporariorum* were collected from tobacco plants, *Nicotiana* sp. grown in the UBC greenhouse. Adults were aspirated into small plastic vials (30 adults/vial) and held for 2 hours prior to release. Sixty unsexed whiteflies were released from two vials at either side of the cage (Figure 2.1).

The experiment was conducted as a completely randomized block design (RCBD) with cages representing the experimental units. Twenty cages were setup in the laboratory with each treatment repeated five times on 3 different days (days=blocking factor) totaling 15 replications per treatment-time combination. The number of adults settled per pepper stand (main crop) and per trap was recorded 1, 2, 3 and 24 h after release and the number of eggs per pepper leaf was counted under a dissecting microscope.

The mean number of adults settled per pepper stand for each cage (main crop) and per trap over time was analyzed as repeated measures ANOVA in SAS Statistics Software (version 9.2) using PROC MIXED. The aim was to compare the mean levels of two responses (mean number of settled adults on main crop and trap) in the presence of the four traps (control, eggplant, squash and yellow sticky traps) over four observation times (1, 2, 3 and 24 h). Treatment, settling location (main crop or trap) and time were fixed factors. Unequal differences in the repeatedly measured time points were accounted for in the model by an autoregressive correlation structure. Model assumptions were verified and found to have normally distributed residuals, centered around zero with constant variance. Significant treatment*location*time interaction effects were further analyzed with a Tukey-Kramer multiple comparison test. The experiment was replicated three times (blocks = random factor) and individual cages (cage = random factor) were the repeatedly measured subjects.

After 24 h, the mean number of eggs per pepper plant for each cage was analyzed for each block-treatment-cage combination in JMP® (version 7.0.1) using the Fit Model Platform. The blocking factor was random and the four levels of the treatment (control, eggplant, squash and yellow sticky traps) were fixed. Tukey-Kramer post-hoc test was used to determine which mean egg counts were statistically significant from each other. The model assumptions were all verified and one outlier was discovered. The model was run with and without the outliers and no changes in results were detected. The residuals were normally distributed, centered about zero, with constant variance. The control treatment of no trap created an unequal proportion of potential landing sites for the whiteflies within cages (e.g. four landing sites in the control cages compared to five landing sites in the cages with traps). To account for this inequality of landing sites, the control data was reduced by 20% to equalize the expected number of whiteflies per plant from one in four to one in five.

2.2.2 Resident whitefly response to trap crops and yellow sticky traps

The effects of traps on resident *T. vaporariorum* were evaluated in a laboratory at the UBC in May 2009 with the goal to determine how whiteflies settled on a host (resident whiteflies) responded to nearby traps. Here, resident whiteflies represented adults that were settled and already present on a plant. To obtain resident adults, pepper seedlings (one leaf/plant) were placed in cages and whiteflies, collected from tobacco plants, were released at the base of each plant at a rate of 30 whiteflies/plant. Whiteflies were left undisturbed for 14 h. Peppers with resident whiteflies were placed in the rear centre of a given cage (Figure 2.2 - Site 1: Pepper with resident whiteflies) and the number of resident adults per pepper were recorded. After recording adult populations on peppers at Site 1, four trap treatments were placed 20 cm in the front centre of the cage (Figure 2.2 - Site 2: Trap). The number of adults at Site 1 and at Site 2 was recorded after 24 h and adults were collected to determine the sex ratio.

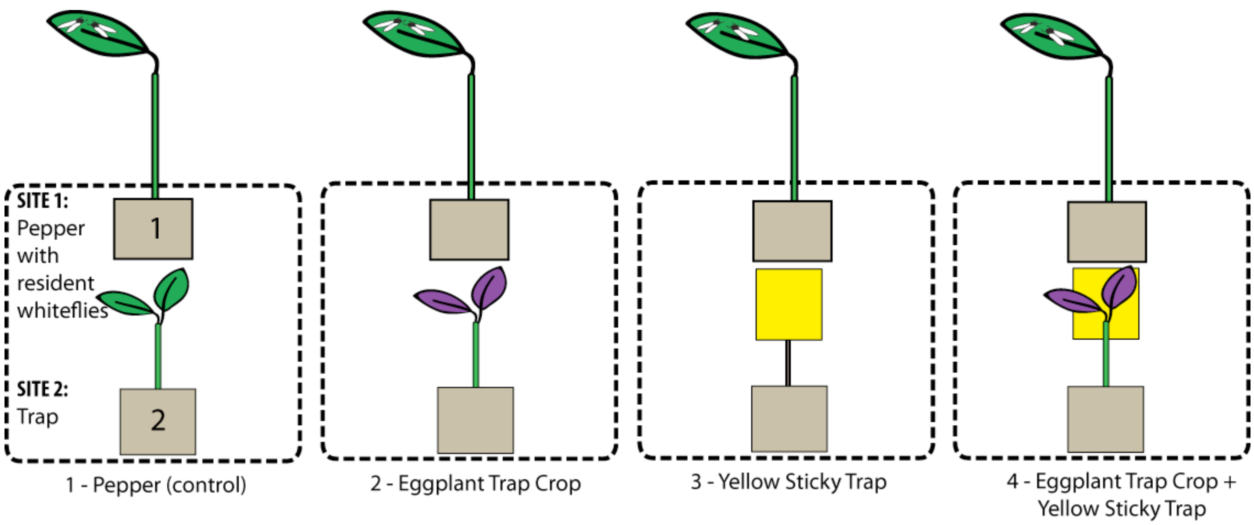

Figure 2.2. Resident whitefly cage bioassay comparing net loss of settled adults after 24 h in the presence of (1) pepper (control), (2) eggplant, (3) yellow sticky trap and (4) eggplant + yellow sticky trap. Site 1 is the location of the pepper with resident whiteflies. Site 2 is the location of the trap.

The experiment was conducted as a randomized complete block design. Treatments were conducted five or six times each day and the experiment was repeated on three occasions (days). New plants and insects were used for each sample and the total number of samples for each treatment was 16. Whitefly count data at time 0 and time 24 h was used to calculate the mean proportion of insects that departed from the original pepper with whiteflies after 24 h and the mean proportion of insects gained on the traps after 24 h.

The mean proportion of whiteflies departed from pepper with whiteflies and gained on traps was separately analyzed as a logistic regression model with SAS Statistics Software (version 9.2) using the PROC GLIMMIX procedure. The logistic regression procedure takes into account different numbers of whitefly introduced at time=0. The treatment effect was a fixed factor. Day, blocks and cages were random factors. Whitefly gender (percentage of insects that were female) was analyzed as a covariate. Model assumptions were verified and two outliers were discovered. The model was run with and without the outliers and no changes in the results were detected.

2.3 Results

2.3.1 Dispersing whitefly response to trap crops and yellow sticky traps

Repeated measures analysis of *T. vaporariorum* adult settling on main crops and traps revealed a significant three-way interaction between the four treatments, two settling locations (main crop or trap) and four time points ($F_{9,408}$= 7.39, p-value < 0.0001) (Table 2.1). Adult settling followed similar trends over time with the highest densities on main crops and traps recorded at 24 h. At 24 h, significantly more whiteflies were recorded on yellow sticky traps than on the eggplant, squash or peppers (main crop) (Figure 2.3). Eggplant had significantly higher densities of whiteflies than squash or peppers (main crop) but less than yellow sticky traps. None of the trap treatments significantly reduced adult population on peppers (main crop) compared to the control (no trap) treatment.

Analysis of whitefly oviposition on main crops after 24 h revealed a significant treatment effect on the mean number of eggs per pepper (main crop) ($F_{3,42}$=4.87, p-value < 0.0054) (Table 2.2). Tukey-Kramer post-hoc tests revealed yellow sticky traps as the only treatment to significantly reduced the number of eggs per main crop (12.53 ± 4.25) compared to the control (no trap) values (30.24 ± 4.25) (Figure 2.4).

Table 2.1. ANOVA table comparing the mean number of ADULT whiteflies settling on main crops and traps after 24 h following 3-way repeated measure analysis.

Effect	Num DF	Den DF	F Value	Pr > F
Trap treatment	3	92.7	78.41	<.0001
Settling location	1	360	414.90	<.0001
Treatment*location	3	200	180.43	<.0001
Location*time	3	398	3.51	0.0153
Time	3	358	90.50	<.0001
Treatment*time	9	400	3.53	0.0003
Treatment*location*time	9	408	7.39	<.0001

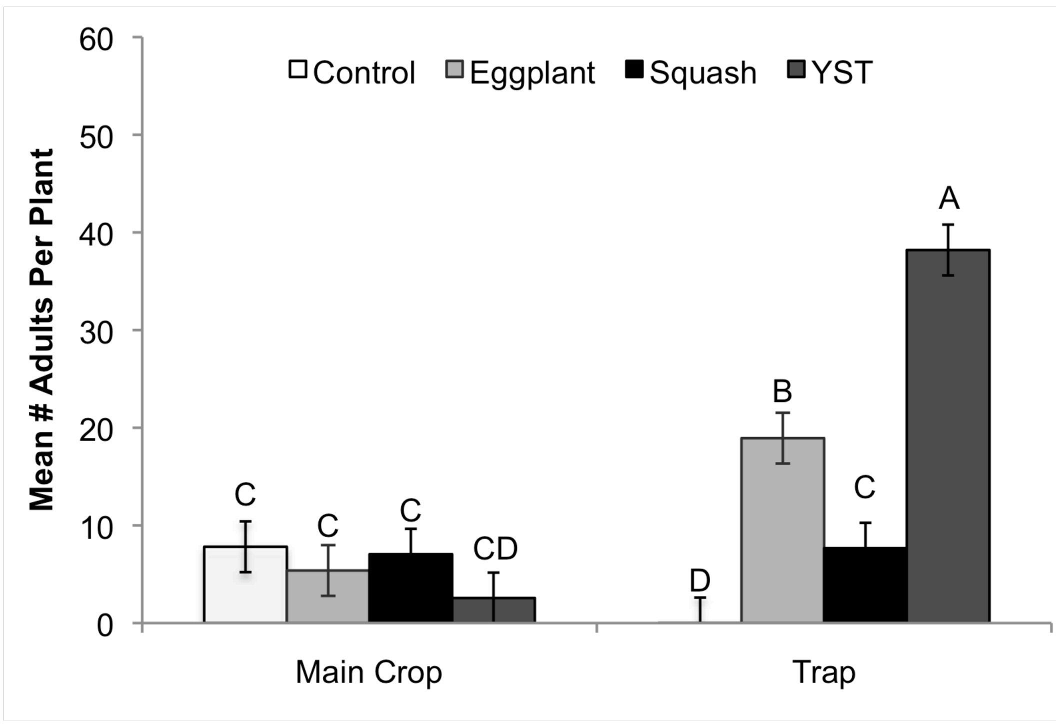

Figure 2.3. Mean (±2SEM) number of ADULT whiteflies per main crop and per trap after 24 h. Means with the same letter are not significantly different (p≤0.05).

Table 2.2. ANOVA results for the mean number of EGGS per main crop after 24 h.

Effect	Numerator Degrees of Freedom	Degrees of Freedom	Denominator Degrees of Freedom	F Ratio	Prob > F
Trap Treatment	3	3	42	4.8656	0.0054

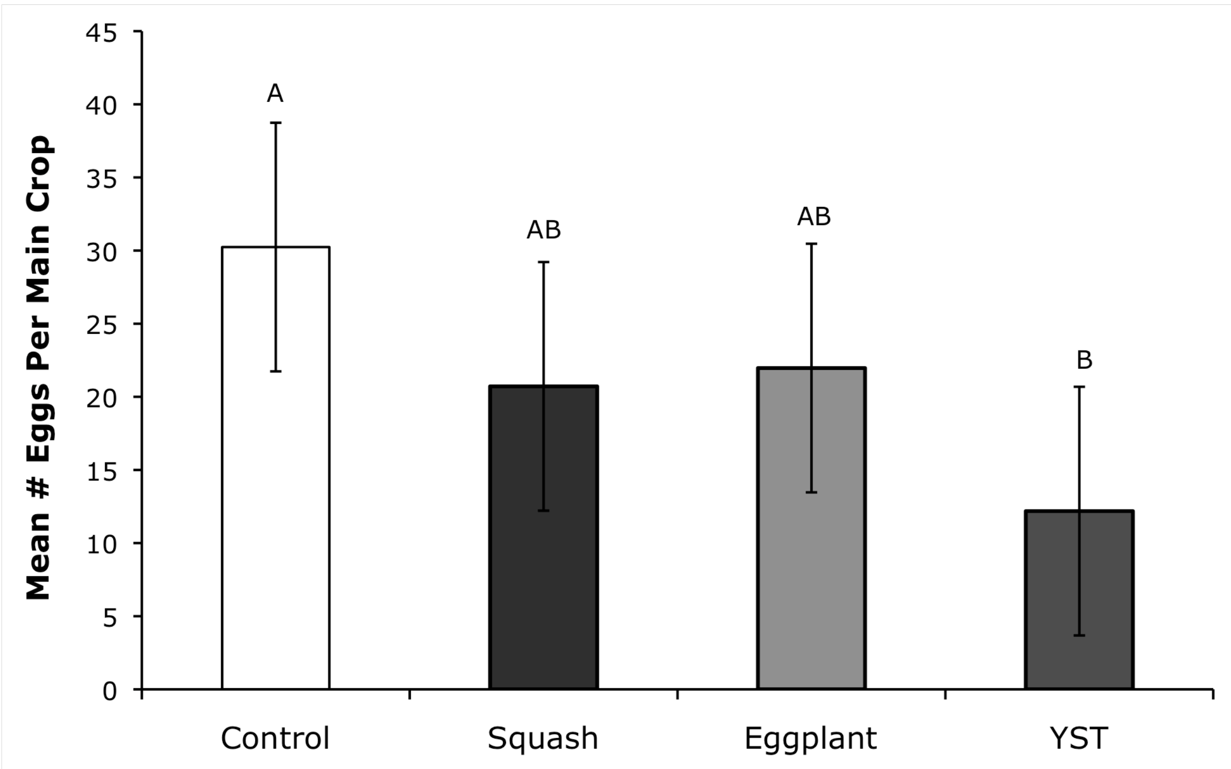

Figure 2.4. Mean (±2SEM) number of EGGS per main crop for each trap treatment (control, squash, eggplant and yellow sticky trap). Means with the same letters are not significantly different (p≤0.05).

2.3.2 Resident whitefly response to trap crops and yellow sticky traps

The continued residence of whiteflies on peppers in close proximity to traps was evaluated at 24 h. Analysis revealed a significant difference between the proportion of whiteflies departing from the original peppers with whiteflies ($F_{3,34}$=3.38, $p < 0.0293$) (Table 2.3). In the pepper (control) treatments, 79% of whiteflies on the original pepper plant at time=0 h were no longer resident on the pepper at 24 h (Table 2.4). Tukey-Kramer post-hoc tests showed that significantly more whiteflies departed from peppers with whiteflies in the YST treatments (0.88±0.08) than in the pepper (control) treatments (0.79±0.12) (Table 2.4).

Comparison of the proportion of whiteflies gained on traps after 24 h demonstrated that eggplant, yellow sticky trap and eggplant + yellow sticky trap treatments had significantly higher proportions of whiteflies than the pepper (control) treatment ($F_{3,34}$ = 42.04, $p < 0.0001$) (Table 2.5). In the pepper (control) treatment, only 16% of the total whiteflies were found on the trap (Table 2.4). Eggplant, eggplant + yellow sticky trap and yellow sticky trap treatments each gained 55%, 71% and 74% respectively of the whiteflies. Tukey-Kramer post-host tests found no difference between the yellow sticky trap and eggplant + yellow sticky trap treatments.

The percentage of female whiteflies on the original peppers and on the traps after 24 h was analyzed as a covariate in the logistic regression model. The results indicated that the gender covariate improved estimates of the trends for the mean proportion of resident whiteflies departing from pepper ($F_{1,34}$=7.99, $p < 0.0078$) (Table 2.3). However, gender was not a significant covariate in the arrival of whiteflies to traps ($F_{1,34}$=2.78, p=0.1047) (Table 2.5). In general, there were more females remaining on peppers with whiteflies when the pepper (control) trap was present. This suggests females were more likely to leave their feeding site than males when eggplant, yellow sticky traps, or eggplant + yellow sticky trap treatments were present.

Table 2.3. GLIMMIX results for the mean proportion of whiteflies departed from peppers with whiteflies 24 h after trap introduction.

Effect	Numerator Degrees of Freedom	Denominator Degrees of Freedom	F Ratio	Prob > F
Trap Treatment	3	34	3.38	0.0293
Gender	1	34	7.99	0.0078

Table 2.4. Tukey-Kramer post-host tests comparing the mean (±2SEM) proportion of whiteflies DEPARTED from pepper with whiteflies after 24 h and the mean (±2SEM) proportion of whiteflies gained on traps. For each column, means with the same letters are not significantly different (P< 0.05).

Treatment	Mean (±2SEM) adults departing from pepper	Mean (±2SEM) adults arriving on trap (±2SEM)
1 - Pepper (control)	0.79±0.12 b	0.16±0.18 c
2 - Eggplant	0.83±0.12 ab	0.55±0.10 b
3 - YST	0.88±0.08 a	0.74±0.14 a
4 - Eggplant + YST	0.87±0.09 ab	0.71±0.16 ab

Table 2.5. GLIMMIX results for the mean proportion of whiteflies that ARRIVED on traps from peppers with whiteflies 24 h after trap introduction.

Effect	Numerator Degrees of Freedom	Denominator Degrees of Freedom	F Ratio	Prob > F
Trap Treatment	3	34	42.04	0.0001
Gender	1	34	2.78	0.1047

2.4 Discussion

Yellow sticky traps and trap crops have been recommended as alternative *T. vaporariorum* greenhouse management tactics (Ferguson *et al.*, 2003). However, there is little experimental evidence of trap crop efficacy within sweet pepper crops and no previous direct comparisons between trap crops and yellow sticky traps are known. Results of the present study with *T. vaporariorum* suggest that yellow sticky traps were the most effective traps for dispersing and resident adults. Here, dispersing whiteflies represents adults that would be moving or searching for host plants, whereas resident whiteflies represented an established population on host plants.

Laboratory evaluations of dispersing adult settling on peppers (main crop) and traps indicated that adults were trapped mostly by yellow sticky traps followed by eggplant but none of the traps significantly reduced adult populations on peppers (Figure 2.3). A possible explanation for the insignificant effect of trap treatment on adult settling per pepper may be the large degree of variation in the data. Another possibility is that, alone, individual yellow sticky traps and trap crops may not be powerful enough tools to significantly reduce adult densities on peppers. Comparison of whitefly oviposition on peppers revealed yellow sticky traps were the only treatment to significantly reduce the number of eggs laid on peppers compared to the control. Based on these experiments, it seems that yellow sticky traps were more effective at trapping and retaining dispersing adults than eggplant and squash. Although neither eggplant nor squash significantly reduced populations on peppers, eggplant trapped significantly more adults than squash indicating that it was a better trap than squash (Figure 2.3). Similar patterns of *T. vaporariorum* attraction to eggplant was found in experiments with poinsettia plants as the main crop (Lee *et al.*, 2009)

Results of the resident *T. vaporariorum* experiment found yellow sticky traps were the only treatment to significantly reduce adult populations on peppers. Eggplant and eggplant + yellow sticky trap treatments did not significantly increase resident whitefly departure from plants. Based on the individual trapping effect of eggplant and yellow sticky traps on dispersing whiteflies (Experiment 2.2.1, Figure 2.3), it was predicted that combining eggplant with a yellow sticky trap would enhance adult trapping. However, the results showed no indication that combining the two traps increased whitefly departure from pepper plants. A possible explanation may be that eggplant blocked the yellow sticky trap thereby decreasing the resident whiteflies line of sight to the yellow sticky traps.

Eggplant's efficacy as a trap crop for adult *T. vaporariorum* is uncertain at this time. Significant trapping of dispersing *T. vaporariorum* on eggplants suggests that eggplant can attract or arrest adults but no significant reductions on peppers were seen. Results of the resident whitefly experiment indicated that settled adults were not significantly pulled away from peppers to eggplant. In a recent paper by Lee *et al.* 2009, the authors identified pest mortality on the main crop as a key factor effecting trap crop. Clearly, more information is required to improve our knowledge of trap cropping for whiteflies. Although the banker plant potential of eggplant was not evaluated in this study, there is previous evidence that banker plants help establish *E. Formosa* or other natural enemy colonies within greenhouses (Stacey, 1977; Hokkanen, 1991; Buitenhuis & Shipp, 2006).

Two important parameters influencing trap crop effectiveness are insect attraction to and arrestment strength of the trap crop in use (Shelton & Badenes-Perez, 2006). *Trialeurodes vaporariorum* attraction to eggplants was compared in the resident whitefly experiment and results indicated that settled adults were not strongly attracted to eggplant compared to pepper. These results contrast experiments by Lee *et al.* (2009), where *T. vaporariorum* movement from infested poinsettia to uninfested eggplant exceeded movement from infested poinsettia to uninfested poinsettia. Variations in main crop species, *T. vaporariorum* populations, and experimental design and conditions may contribute to the different results obtained in this study and those results obtained by Lee *et al.* 2009. Whitefly host plant history, adaptation and preference was described by Lee *et al.* 2009 as a key factor affecting trap crop efficacy and may explain the differences in results obtained with peppers and poinsettias.

Results of the resident *T. vaporariorum* experiment found that 79% of whiteflies on the original pepper (Site 1) in the control treatment had departed from the plant after

24 h. This indicates that peppers did not exhibit strong arrestment strengths on adults. The whitefly populations used in these experiments were collected from a high-ranking host, tobacco. A high departure rate from peppers supports previous findings that on low-ranking hosts, such as peppers, whiteflies feed less and depart more frequently (van Lenteren & Noldus, 1990). Resident *T. vaporariorum* departure from peppers indicated females were more likely to leave peppers in the presence of yellow sticky traps, eggplant and eggplant + yellow sticky traps than in the presence of the control treatment (pepper). Further gender-specific evaluation is necessary to improve our understanding of whitefly responses to traps. The arrestment strength of eggplant was not implicitly tested in this study. Future experiments exploring whitefly attraction versus arrestment on trap crops and main crops are recommended as a means of improving our understanding of the mechanisms governing trap crop control of *T. vaporariorum.* For example, if whiteflies arrive to pepper and eggplant at equal frequencies then comparing departure rates may help elucidate the arrestment strength of trap crops.

Although previous reports describing the strong role vision plays in *T. vaporariorum* host finding exist (Coombe, 1982; van Lenteren & Noldus, 1990), this current study predicted adult whiteflies would be equally attracted to both yellow sticky traps and high-ranked hosts such as eggplant. One explanation for higher trapping rates of whiteflies on yellow sticky traps compared to trap crops may simply be that adults responded more to the visual cues of yellow sticky traps than trap crops. However, a limitation of this study was the sticky nature of the yellow sticky traps. For both eggplant and squash, whiteflies could depart from the plants after landing but the stickiness of the yellow sticky traps reduced departure. It is recommended that in future studies the sticky nature of the traps be removed by covering traps with clear plastic (see Chapter 5).

In conclusion, results showed yellow sticky traps to be more effective traps than trap crops. Additional research into *T. vaporariorum* management using trap crops is needed to improve our understanding of the functioning of this system. Exciting advancements in the study of insect-plant interactions are increasing our knowledge of insect olfactory responses. However, the role of vision, especially in whiteflies, cannot be underestimated. Further investigation of whitefly visual responses to UV materials, flower trap models and LEDs, may offer avenues of increased trapping (Chu *et al.*, 2003; Mutwiwa *et al.*, 2005; Mainali & Lim, 2008). Furthermore, research combining yellow sticky traps and trap crops with other control strategies is necessary to improve our understanding of whitefly responses to traps in the context of specific host plants.

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Chapter 3[*] The effects of reduced-risk sprays on greenhouse whitefly (*Trialeurodes vaporariorum)* settling and oviposition behaviours

3.1 Introduction

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera, Aleyrodidae) is a notorious greenhouse pest. The use of reduced-risk sprays (RRSs) such as insecticidal soaps, vegetable oils and plant extracts represent alternative pest control tactics that are considered to have fewer health and environmental impacts than conventional pesticides (Fraser, 2005). A number of reduced-risk sprays have been tested against *T. vaporariorum* and *Bemisia tabaci* (Gennadius) as toxicants, repellents, deterrents or antifeedants (Larew & Locke, 1990; Mele *et al.*, 1992; Buta *et al.*, 1993; Simmonds *et al.*, 2002; Choi *et al.*, 2003; Chiasson *et al.*, 2004; Pavela & Herda, 2007; Schuster *et al.*, 2009). Despite numerous reports of reduced-risk spray efficacy against whiteflies, commercial greenhouse application of these alternative sprays is low.

Manipulating whitefly behaviour using reduced-risk sprays to prevent adult settling and oviposition on plants has been postulated as a method of reducing insect pest densities and damage to crops (Foster & Harris, 1997; Cook *et al.*, 2007). From previous evaluations of reduced-risk sprays and whiteflies, it is not always clear if whiteflies are responding to sprays over long-distances (no direct contact with source material) or short-distances (direct contact with source material). Repellence, with regard to the whitefly, is defined here as the insects' directed movement away from a source of a stimulus without direct contact. Deterrence is defined as a change in whitefly settling resulting from short distance tactile contact with materials. Most research indicates that extracts, soaps and oils act as deterrents which affect *T. vaporariorum* and *B. tabaci* behaviour only after direct contact with the materials (Liu & Stansly, 1995). However, other research has shown that whiteflies are repelled over long-distances by some reduced-risk sprays (Gorski, 2004; Zhang *et al.*, 2004).

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The objective of the following chapter was to explore whitefly responses to reduced-risk sprays and to determine from what distance these materials affect *T. vaporariorum* and how significantly they alter settling and oviposition behaviours. Specifically, the interest was to evaluate if whiteflies can be repelled or pushed away from pepper plants using reduced-risk sprays. This was first accomplished by evaluating the toxicity of reduced-risk spray vapours with the assumption that toxic vapours may have a repellent effect on whiteflies. Next, whitefly settling on peppers with toxic and less toxic vapours was compared. In subsequent experiments, direct contact with reduced-risk sprays was evaluated to compare short-distance settling deterrence. In the final experiment, sprays were applied to yellow sticky traps to determine if their vapours of affected whitefly entrapment on yellow sticky traps.

3.2 Materials and Methods

Plant and Insect Material: Pepper seedlings (c.v., "Forever", Enza Zaden), were obtained from Houweling Nurseries (Delta, BC) at an age of four weeks. Plants were moved to the Horticulture Greenhouse at the University of British Columbia (UBC) and grown under natural daylight conditions within the greenhouse. Commercial plants were irrigated and fertilized daily with a dilute fertilizer solution of 100 ppm of 15-5-15 NPK Cal-Mag (Scotts, Peters Excel). *Trialeurodes vaporariorum* adults were collected from a natural population established in the Horticulture Greenhouse at UBC. Adults of mixed age and sex were aspirated from tobacco (*Nicotiana* sp.) into holding vials approximately 2 h before use in the experiments.

3.2.1 Fumigation toxicity of clove, olive, rosemary and white thyme oil against adult *T. vaporariorum*

The four reduced-risk sprays selected for testing on adult whiteflies were clove oil, olive oil, rosemary oil and white thyme oil. Olive oil (Safeway Select, Extra Virgin) was selected as the control treatment under the assumption of having no effect on whitefly behaviour. Clove oil (Aura Cacia), rosemary oil (Intarome TO, Spanish

Rosemary Lot # 02/25/11MB) and white thyme oil (Aura Cacia) were selected based on previous indications of whitefly toxicity (Choi *et al.*, 2003). Experiments were conducted in a laboratory in July 2008 using a fumigation bioassay arena made from a 1 L clear plastic container (Figure 3.1). Conditions in the lab were approximately 24±3°C, 45% RH with a photoperiod of 12:12 (L:D).

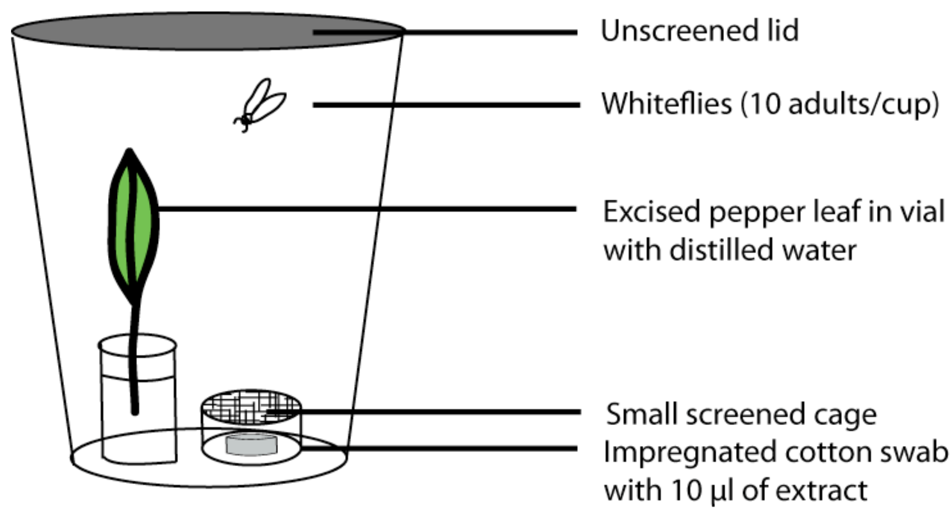


Figure 3.1. Closed fumigation chamber (1 L) comparing clove oil, olive oil, rosemary oil and white thyme oil vapour toxicity against adult whiteflies.

Each arena held one excised pepper leaf in a vial of distilled water, ten adult whiteflies and a reduced-risk spray-treated cotton swab covered with a screened cage. Pepper leaves were provided as a food source and a landing site for the adults. Leaves of similar size and age were excised from whole plants and placed immediately in water. Ten microliters of treatment were applied directly to cotton swabs. Treated swabs were placed under a screen to prevent any direct contact between oils and whiteflies. Adult *T. vaporariorum* were collected from tobacco and held for 2 h prior their release. Ten whiteflies were released from collection vials in each container and container lids were quickly secured to prevent whitefly escape. Adult mortality within the cages was determined 24 h after treatment. Whiteflies were considered dead if their appendages did not move following contact.

The experiment was conducted as a randomized complete block design. Each treatment was conducted three times a day and replicated on three separate days (total of N=9). Adult percent mortality was analyzed as a logistic regression in JMP (version 7.0.1) using the Fit Model Platform with a GLM personality and a binomial distribution. Post hoc contrasts of mean percent mortality were used to identify significant differences between treatments. Assumptions of the logistic regression model were met. The residuals showed no trends or outliers.

3.2.2 *Trialeurodes vaporariorum* settling over time on pepper stands equipped with rosemary or olive oil fumigation chambers

In Experiment 3.2.1, rosemary oil and olive oil were selected as toxic and less toxic oils respectively. It was hypothesized that vapours from a toxic oil (rosemary) would repel whiteflies from settling on nearby peppers compared to the vapours from a less toxic oil (olive). To test this hypothesis, no choice bioassays were conducted in BioQuip® Bugdorm-2 (60 x 60 x 60) cages in two adjoined laboratory rooms at UBC from August to September 2008 (Figure 3.2). Initially, this experiment was run as a two choice test but due to concerns about vapour mixing no choice tests were used. The experiment was conducted in two adjoining rooms to allow for similar conditions yet avoiding volatile mixing between rosemary and olive oils. The room conditions were approximately 23±2°C, 45% RH with a photoperiod of 12:12 (L:D). A plant stand with two pepper leaves and a fumigation chamber were placed in the center back of each cage. Leaves were selected from six-month old peppers to ensure leaf age classes were cut from similar growing points with comparable surface areas. For each plant stand, two excised leaves were placed immediately in vials with distilled water. Vials were secured to the stands at height = 25 cm. One hundred microliters of either rosemary oil or olive oil was applied directly to cotton swabs. Treated cotton swabs were placed in the fumigation chambers to prevent any direct contact between oils and whiteflies. Fumigation chambers were secured to the stands at height = 15 cm. Adult whiteflies were collected from tobacco and held for ~ 2 h prior to their release. Thirty whiteflies were released in each cage approximately 20 cm from the pepper stand. Whitefly settling on peppers with toxic and less toxic vapours was measured 1, 2, 3, 4 and 5 h after release.

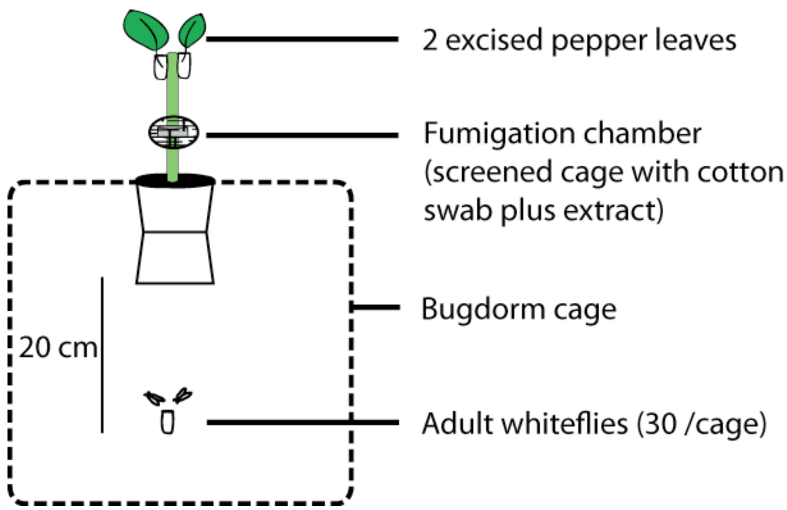


Figure 3.2. Cage bioassay evaluating whitefly settling on pepper stands equipped with rosemary or olive oil fumigation chambers

Treatments were randomly assigned a room and were replicated eight times for the first day and five times for the second day (total sample size = 13). Cages represented the experimental units. The rooms used for the treatments were switched between replicates. The mean number of whiteflies settling on peppers in the presence of rosemary and olive oils over time was analyzed as a repeated measures two-way analysis of variance using JMP (version 7.0.1). The Fit Model Platform was used with the repeated measures functions. Model assumptions were verified.

3.2.3 *Trialeurodes vaporariorum* settling and oviposition on pepper leaf disks treated with reduced-risk sprays

The short-distance effects of reduced-risk sprays on whitefly settling and oviposition was measured using small container arenas in a laboratory at UBC in March 2009 (Figure 3.3). The treatments evaluated were Hot Pepper Wax™ (capsaicin and other capsaicinoids: Hot Pepper Wax Inc), olive oil (Safeway Select, Extra Virgin), rosemary oil (Intarome TO, Spanish Rosemary Lot # 02/25/11MB) and Safer's Natural Insecticide (Safer's Soap). Hot Pepper Wax™ and Safer's Soap were selected as two commercial products that claim to control whiteflies. Olive oil and rosemary were selected based on their use in earlier experiments. All treatments were mixed with 1% Tween 20 and distilled water to obtain a 2% concentration of product. The control was 1% Tween 20 in distilled water.

Figure 3.3. Small container (250 ml) bioassay testing whitefly settling, oviposition and mortality on treated leaf disks.

No choice experiments were conducted in clear plastic containers (250 ml). Previous reports using similar arenas recommend no choice tests as effective and efficient methods of testing anti-settling properties of products against *B. tabaci* (Schuster *et al.*, 2009). Each container was one experimental unit and contained one treated or untreated leaf disk (3 cm diameter). The abaxial side of leaf disks was placed on containers so that leaf undersides were presented to insects within the arena. Each disk was covered with moist filter paper (Whatman® Number 1 [3 cm diameter]) to reduce drying. A dry filter paper was placed inside the container to absorb moisture and prevent adult mortality. Small holes were punctured on all sides of the containers to permit air exchange. Adult whiteflies of mixed age were collected from tobacco and held for 2 h prior to their release. The undersides of ten leaf disks were sprayed with 5 ml of the 2% treatment solution. Disks were air dried for 20 minutes before use. Once the arenas were assembled, whiteflies were introduced to the containers through a hole in the side. The laboratory conditions were 23±2°C, 45% RH with a photoperiod of 12:12 (L:D). Whiteflies were gently tapped from the release vials and a cork stopper was inserted into the hole. The arenas and whiteflies were left undisturbed for 24 h. The number of adults settled per disk, the number of dead whiteflies per container and the number of eggs per disk was recorded at 24 h.

The experiments were conducted as a randomized complete block design (RCBD). Each treatment was replicated ten times a day on two separate days (total of N=20). The number of adults settled per disk and the number of dead adults per container were used to calculate the mean percentage of total whiteflies settled per disk after 24 h. Adult percent settling was analyzed in JMP (version 7.0.1) with logistic regression using the Fit Model Platform. Post hoc contrasts of mean percent settling were used to identify significant treatment effects. Assumptions of the logistic regression model were met. The residuals showed no trends or outliers.

The mean numbers of eggs laid on disks per treatment were analyzed using analysis of variance in JMP (version 7.0.1). Replicates were random factors and the treatments were fixed factors. Tukey-Kramer post-hoc tests were used to identify significant treatment effects. The model assumptions were verified and one outlier was identified. The model was run with and without the outlier and no major changes were seen. Analysis of the full data set is provided. The residuals were normally distributed and centered about zero with constant variance.

3.2.4 *Trialeurodes vaporariorum* trapping on reduced-risk spray treated and untreated yellow sticky traps

The objective of this experiment was to determine if whitefly trapping on yellow sticky traps could be increased or decreased by the presence of reduced-risk sprays. A two choice test comparing whitefly entrapment on treated and untreated yellow sticky traps was used to evaluate whitefly responses to visual attractants treated with reduced-risk sprays (Figure 3.4). The four treatments tested included Hot Pepper Wax™, lemon oil (Aura Cacia), olive oil (Safeway Select, Extra Virgin) and white thyme oil (Aura Cacia). Hot Pepper Wax™ and lemon oil were selected based on previous reports indicating that they may increase whitefly settling on plants or entrapment on yellow sticky traps (Gorski, 2004; Schuster *et al.*, 2009). Olive oil and white thyme oil were selected based on tests done in the laboratory that indicated that they might reduce whitefly settling (Experiment 3.2.3 for olive oil and Experiment 3.2.1 for white thyme oil). Each treatment was independently compared to a control in a two choice test.

Figure 3.4. Greenhouse trial comparing whitefly entrapment on yellow sticky traps treated with and without reduced-risk sprays.

The experiments comparing whitefly entrapment on treated and untreated yellow sticky traps were conduced in the UBC Horticulture Greenhouse in March 2009 (Figure 3.4). Yellow sticky traps (Horiver, Koppert) were cut to 100 cm^2 and sprayed with extract solutions. Treated traps were secured to a stand with a clothes peg so that sticky trap tops were at a height of 45 cm. Ten pairs of treated and untreated yellow sticky traps (45 cm between pairs) were evenly distributed on two benches (14 x 1.5 m) in the greenhouse. On each bench multiple plant species were grown and plants were highly infested with *T. vaporariorum.* All extracts were mixed with 1% Tween® 20-distilled water solution to obtain a 50% concentration. The extract solutions (0.5 ml) were evenly sprayed on the front and back of each trap and traps were air dried for 20 minutes before being placed in the greenhouse. Only one treatment was investigated per day to prevent volatile mixing across benches. Ten paired choice (treated and untreated yellow sticky traps) combinations were arranged for each day and the experiment was replicated on two separate days for each treatment (total sample size = 20). The number of whiteflies per trap was measured after 24 h.

The mean number of whitefly adults on treated and untreated sticky traps after 24 h was calculated and analyzed as a two-sample paired t-test with JMP (version 7.0.1). Statistics were carried about using a matched paired analysis. The mean number of adult whiteflies per trap was determined. Model assumptions of equal variances and additivity between treatments were all verified.

3.3 Results

3.3.1 Fumigation toxicity of clove, olive, rosemary and white thyme oil against adult *T. vaporariorum*

The fumigation toxicity of four reduced-risk sprays against adult whiteflies was compared and mean percent mortality (±2SEM) is presented in Figure 3.5. The analysis revealed a significant difference in percent mortality between treatments (chi-square$_3$=115.06, $p < 0.0001$). Post hoc contrasts revealed that rosemary oil and white thyme oil had significantly higher mortalities than olive oil and clove oil. Severe phytotoxicity of pepper leaves was noticed in the clove oil treatments.

3.3.2 *Trialeurodes vaporariorum* settling over time on pepper stands equipped with rosemary or olive oil fumigation chambers

Results of whitefly settling on peppers in the presence of rosemary versus olive oil were analyzed using a two-way analysis of variance with repeated measures of cages over 1, 2, 3, 4 and 5 h (Figure 3.6). The treatment by time interaction was not significant, $F_{4,21}$=0.19, p = 0.4244. The main effect of treatment (rosemary versus olive oil control) was also not significant $F_{1,21}$=0.05, p = 0.2832. Analysis revealed a significant effect for time $F_{4,21}$=4.55, p < 0.0001. Post hoc contrasts between time points indicated that whitefly settling on pepper plants was significantly higher at time = 3 h than whitefly settling at time = 1 hr.

3.3.3 *Trialeurodes vaporariorum* settling and oviposition on pepper leaf disks treated with reduced-risk sprays

Whitefly settling and oviposition per leaf disk was compared between treatments (control, Hot Pepper Wax™, olive oil, rosemary oil and Safer's Soap). There were significant differences in the effects of treatments on the proportion of total whiteflies per cage that settled after 24 h (X^2_4=34.14, $p \leq 0.0001$). Post hoc contrasts revealed that more adults settled on leaf disks treated with Hot Pepper Wax™ and the control than on disks treated with olive oil, rosemary oil and Safer's Soap (Figure 3.7). Analysis of variance of the mean number of eggs per disk indicated significant differences between treatments ($F_{4,94}$=7.12,$p < 0.0001$) (Figure 3.7). Tukey-Kramer post-hoc tests showed that significantly more eggs were laid on disks treated with Hot Pepper Wax™ (94.50±18.48) than on olive oil (39.55±18.48) and Safer's Soap (43.73±18.48) (Figure 3.7).

3.3.4 *Trialeurodes vaporariorum* trapping on RRS treated and untreated yellow sticky traps

Whitefly trapping on yellow sticky treated with reduced-risk sprays was evaluated in a greenhouse after 24 h. Although all treated traps had fewer whiteflies compared to the control traps, the results revealed that none of the oils significantly reduced adult trapping on yellow sticky traps (Table 3.1).

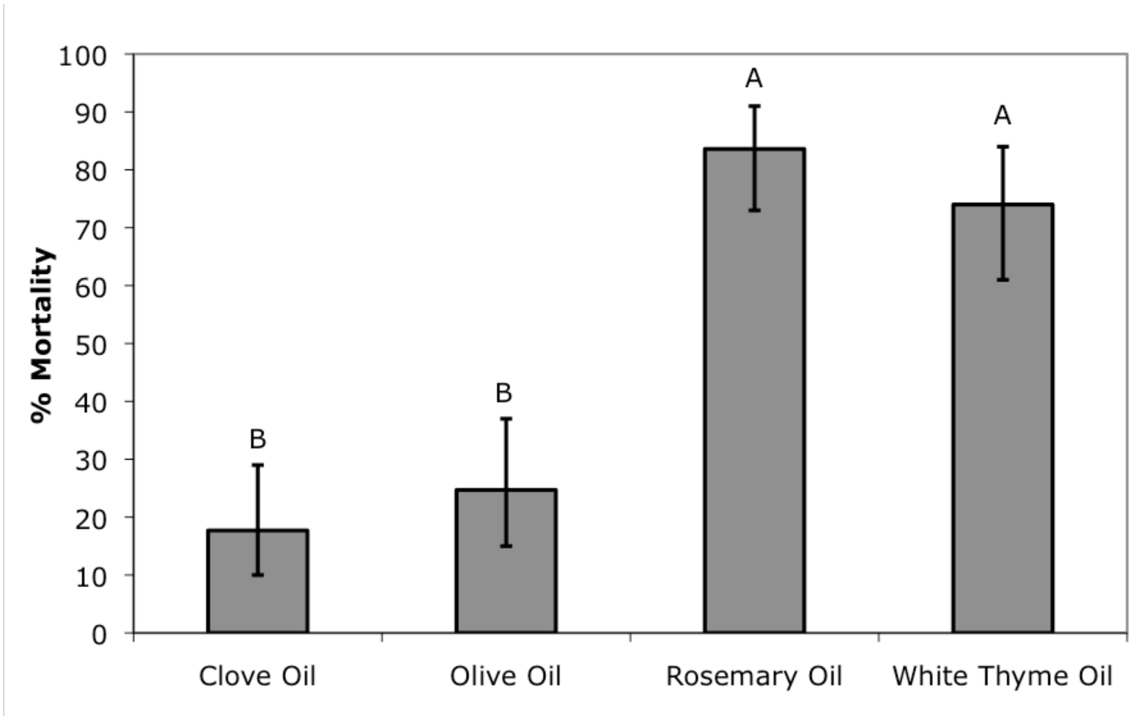


Figure 3.5. Mean adult percent mortality (±2SEM) following 24 h long-distance contact with treatment vapours. Means with the same letter are not significantly different (p≤0.05).

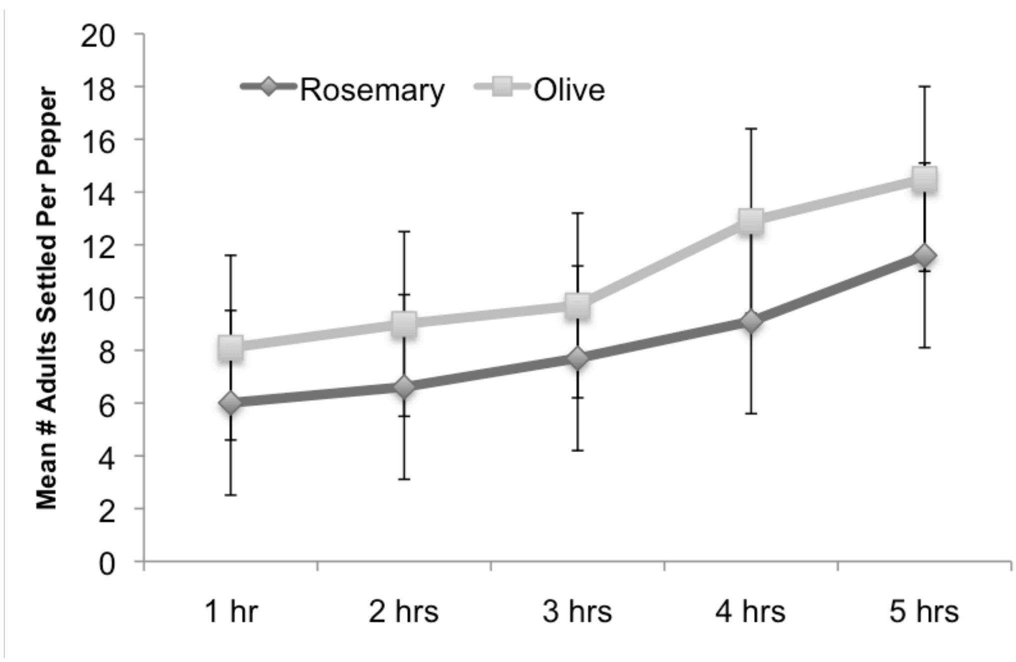
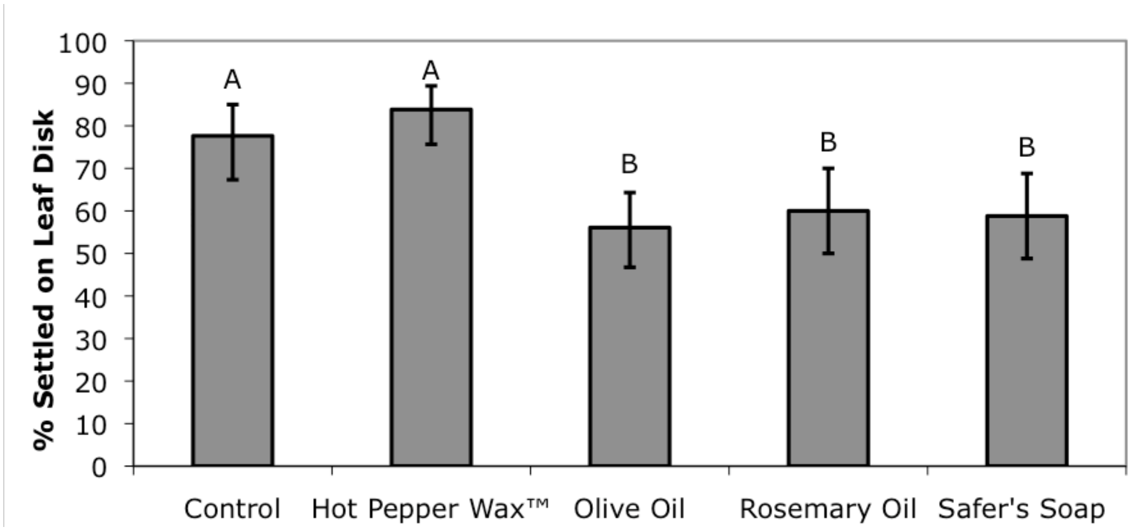


Figure 3.6. Mean (±2SEM) number of whiteflies settled on pepper plants equipped with rosemary or olive oil fumigation chambers. An overlap of the error bars indicates no significant difference between means (p≤0.05).



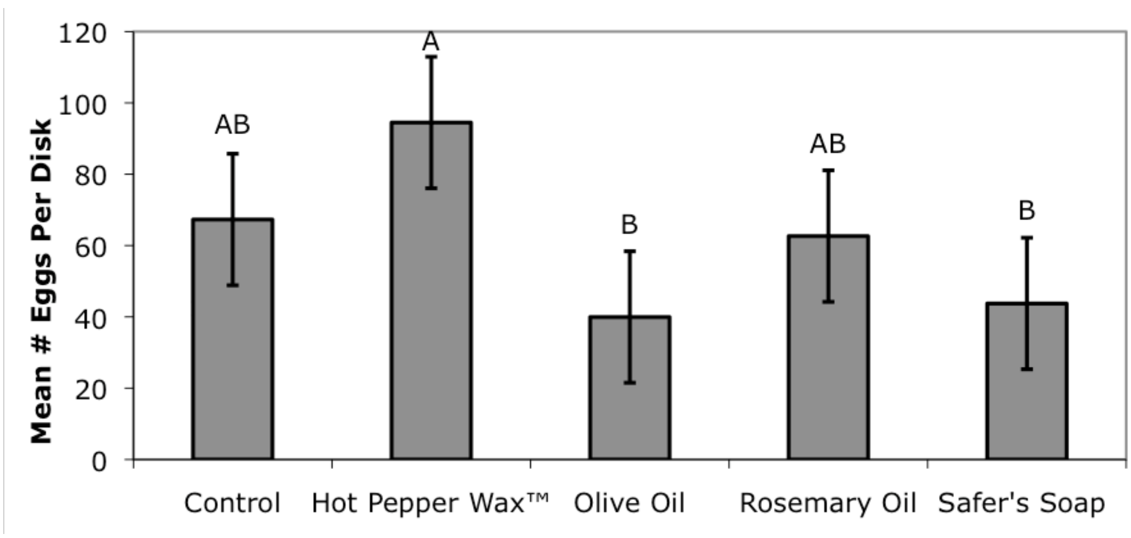


Figure 3.7. Mean (±2SEM) percentage of whiteflies settled per disk and mean (±2SEM) number of eggs per disk following short-distance contact with treatments. Means followed by the same letter are not significantly different ($p \leq 0.05$).

Table 3.1. Paired t-test comparing mean number of *T. vaporariorum* caught on treated and untreated yellow sticky traps.

YST Treatment	Replicates	2 Choice	Mean (±2SE) number of adults	t-value	P-value
HPW	20	Treated	136.75±31.8		
		Untreated	160.45±31.8	-1.49	0.1526
Lemon Oil	20	Treated	126.50±27.9		
		Untreated	155.60±27.9	-2.08	0.0509
Olive Oil	20	Treated	148.37±17.9		
		Untreated	159.16±17.9	-1.21	0.2421
White Thyme Oil	20	Treated	176.10±22.34		
		Untreated	180.35±22.34	-0.38	0.7077

3.4 Discussion

Fumigation tests indicated that rosemary and white thyme oil vapours were more toxic to *T. vaporariorum* adults than with olive and clove oil vapours. A previous evaluation of 53 plant extracts tested against *T. vaporariorum* speculated that fumigation toxicity was due to volatile plant compounds that penetrate insect cuticles via the respiratory system (Choi *et al.*, 2003). Based on results of fumigation experiment 3.2.1, it was theorized that toxic vapors might repel adult *T. vaporariorum* and reduce settling on nearby sweet peppers. However, comparisons of adult settling on peppers in the presence of a toxic (rosemary) and a less toxic (olive) oil indicated that settling was not reduced by rosemary oil compared to olive oil. Therefore, rosemary oil vapours did not repel or push whiteflies away from sweet pepper plants.

Adult settling on pepper leaf disks treated with reduced-risk sprays was evaluated using a no choice arena (Experiment 3.2.3). A 2% spray concentration of olive oil, rosemary oil and Safer's Soap significantly decreased adult setting on disks by 28%, 23% and 24% respectively. Oviposition on treated leaf disks was not significantly reduced by any treatment. *Trialeurodes vaporariorum* entrapment on treated and untreated yellow sticky traps was evaluated to further test adult responses to long-distance plant oil vapours. In contrast to previous reports of extracts increasing whitefly entrapment on yellow sticky traps, treatment of traps with Hot Pepper Wax™, lemon oil, olive oil and white thyme oil did not significantly increase nor decrease adult trapping on traps (Gorski, 2004). Differences between this work and Gorski's (2004) may be due the doses of extracts used in the experiments. Gorski (2004) applied 0.1 ml of extract using a paintbrush to a small part of the yellow sticky trap. In contrast, 0.5 ml of 50% RRS concentration was sprayed directly on the yellow sticky traps. Previous results of work done with cabbage loopers and plant compounds demonstrated that looper attraction and deterrence was strongly affected by the dose of treatment (Akhtar *et al.*, 2007). The results of this current study further demonstrate that adult *T. vaporariorum* settling on traps was not strongly influenced by odors of reduced-risk sprays.

Understanding how whiteflies respond to plant extracts and oils over long- and short-distances provides insight into how whitefly behaviour can be manipulated for improved control within greenhouses. Previous reports of reduced-risk spray treatment of *T. vaporariorum* and *B. tabaci* use repellent, deterrent and antifeedant as the terminology to describe reduced adult settling (Liu & Stansly, 1995; Simmonds *et al.*, 2002; Zhang *et al.*, 2004; Pavela & Herda, 2007). In most cases, the long- or short-distance effects of reduced-risk sprays on behaviour are not specifically tested, except for Zhang (2004) who demonstrated long-distance (no contact) effects of ginger oil on *B. tabaci*. Fumigation studies represent one method of evaluating long-distance toxicity of reduced-risk spray but generally these papers report mortality and not evaluate behaviours such as settling (Choi *et al.*, 2003; Calmasur *et al.*, 2006).

Natural and synthetic oils have a long history as insect and mite control tactics. Short-distance deterrence (reduced settling following direct contact with source material) of reduced-risk sprays towards both *T. vaporariorum* and *B. tabaci* has been reported for plant extracts, plant oils, horticultural oils, insecticidal soaps and pesticides (Larew & Locke, 1990; Liu & Stansly, 1995; Isaacs *et al.*, 1999; Simmonds *et al.*, 2002; Pavela & Herda, 2007; Schuster *et al.*, 2009). Some advantages of oils over conventional pesticides include little or no resistance by pests, reduced effects on natural enemies, ease of use, and increased safety for handlers and farm workers (Liang & Liu, 2002).

In conclusion, results of these experiments suggest the greatest modification to *T. vaporariorum* settling behaviour resulted from direct contact with olive oil, rosemary oil and Safer's Soap. Long-distance repellence by plant extracts was not demonstrated. Future testing of olive oil toxicity against developmental stages of *T. vaporariorum,* oil phytotoxicity, effects on natural enemies and dose responses are warranted. Furthermore, additional studies of olive oil, rosemary oil and Safer's Soap as reduced-risk sprays are necessary to examine how these materials could be combined with other *T. vaporariorum* control tactics.

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Chapter 4[*] Antixenosis: The effect of plant resistance on greenhouse whitefly (*Trialeurodes vaporariorum)* settling and oviposition behaviours on sweet peppers

4.1 Introduction

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Hemiptera, Aleyrodidae), is a major agricultural pest of greenhouse vegetable and ornamental crops. Plant resistance is considered one of the most potent, economical and effective means of reducing plant diseases and insect damage (De Ponti *et al.*, 1990)**.** Previous accounts from growers and the scientific literature have indicated that whiteflies demonstrate distinct preferences between sweet pepper cultivars (Laska *et al.*, 1982; van Lenteren *et al.*, 1989; Lei *et al.*, 1999; Lei *et al.*, 2001). Although plant resistance to *T. vaporariorum* has been recommended as a simple strategy to improve whitefly control, very little information is available to growers about integrating plant resistance into current whitefly management programs.

Plant resistance to insects is attributed to three mechanisms: antixenosis, antibiosis and tolerance (Smith, 1989; Cook *et al.*, 2007). Antixenosis describes plant traits that modify insect preference behaviours to confer non-preference. Antibiosis describes plant traits that negatively affect insect biology (fecundity, developmental time, etc). Plant tolerance occurs when genetic qualities of a plant enable it to recover or withstand herbivore damage. In monocropped systems, insect non-preference (antixenosis) is not generally considered a valuable resistance character because without options, insects will feed on what is available (De Ponti *et al.*, 1975). However, despite limitations in monocropped systems, antixenosis may have greater effects in diverse agriculture systems where insects are provided a choice between hosts. For example, previous work combining trap crops with insect resistant cultivars of cotton, soybean and rice demonstrated significant improvement in pest control (Smith, 1989).

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[*] A version of this chapter will be submitted for publication. Moreau, T.L. and M.B. Isman. 2010. The effect of plant resistance on whitefly settling and oviposition behaviours on sweet peppers.

Four grades of plant resistance to insects have been described (Berlinger, 1986). These grades include: completely resistant plants (plants are not attacked by pests), resistant plants (plants support some levels of pests but economic thresholds are not exceeded), partially resistant plants (economic thresholds are exceeded but late in the season), and susceptible plants (economic thresholds are exceeded early in the season and pest populations require intensive control). Although complete plant resistance to insects would be ideal for pest management the use of plants that exhibit partial resistance is generally more common (De Ponti *et al.*, 1990).

Variation in host plant preference and performance by *T. vaporariorum* between and within plant species has been investigated for many greenhouse crops (Laska *et al.*, 1982; De Ponti *et al.*, 1990; van Lenteren & Noldus, 1990; Lei *et al.*, 1999). Previous research ranked whitefly host preference and performance from high to low on cucumber > tomato = gerbera > sweet pepper (Lei *et al.* 2001). Although sweet peppers (*Capsicum annuum*) are considered to be one of *T. vaporariorum's* least preferred hosts, whitefly outbreaks in monocropped sweet pepper greenhouses are common.

The objective of these experiments was to evaluate whitefly preferences between sweet pepper cultivars as a potential modifier of whitefly behaviour. Whitefly settling and oviposition was compared using two choice and no choice assays. Two no choice methodologies were further evaluated to test the effects of cultivars and bioassay type on whitefly responses. The specific research questions were as follows:

1. On which pepper cultivars do adult whiteflies prefer to settle and oviposit?
2. Does plant resistance elicit a strong behavioural response from adult whiteflies?

4.2 Materials and Methods

Whitefly preference between commonly grown greenhouse sweet pepper cultivars was initially evaluated in a greenhouse using multiple choice and two choice tests. Results of the preliminary tests indicated some differences in settling between pepper cultivars. However, further evaluation did not produce repeatable results. Due to inconsistencies obtained from these tests and the high cost associated with running them, the research direction shifted to laboratory two choice and no choice bioassays. Insect preference (antixenosis) refers to discrimination amongst suitable hosts and implies the use of choice tests (Storeck *et al.*, 2000). The study of insect performance (antibiosis) on plants most often utilizes no choice tests. Although, the objectives were to evaluate whitefly preferences between pepper cultivars, there was interested in exploring the variation that I was seeing in preliminary tests and therefore conducted both choice and no choice tests as a means of comparing responses between methodologies.

Plant and Insect Material For Choice and No Choice Tests

Pepper seedlings (c.v., "Fascinato" (Red), "Orangery" (Orange) and "Baselga" (Yellow)) were obtained from Houweling Nurseries (Delta, BC) at an age of four weeks. Plants were moved to the Horticulture Greenhouse at the University of British Columbia (UBC) and grown under natural daylight conditions. Pepper plants were irrigated and fertilized daily with a dilute fertilizer solution of 100 ppm of 15-5-15 Cal-Mag (Scotts, Peters Excel). *Trialeurodes vaporariorum* were collected from a natural population established in the UBC Horticulture Greenhouse. Adults of mixed age and sex were aspirated from tobacco (*Nicotiana* sp.) plants approximately 2 h before their use in experiments.

4.2.1 Two choice tests with excised pepper leaves

Whitefly settling on excised leaves of three pepper cultivars (c.v., "Baselga", "Fascinato" and "Orangery") was evaluated using two choice bioassays in BioQuip® Bugdorm-2 (60 x 60 x 60 cm) cages in a windowless laboratory under fluorescent lights at UBC in December 2008. Experimental plant stands for the two choice assays consisted of four pepper leaves (two leaves/cultivar) placed in vials with water (Figure 4.1). Vials were secured to a vertical stand that held leaves at a height of 30 cm. The laboratory conditions were approximately 23±2°C, 45% RH with a photoperiod of 12:12 (L:D). Cages represented the experimental units and one pepper stand was arbitrarily placed in the centre of each cage. Three two choice tests were conducted and the treatments included (1) Baselga versus Fascinato, (2) Baselga versus Orangery, and (3) Fascinato versus Orangery.

Figure 4.1. Two choice plant stands comparing whitefly settling and oviposition on two pepper cultivars (two leaves per cultivar).

Leaves, of similar size and shape, were excised from similar growing points on five-week old pepper plants and placed in warm water. Excised leaves were then transferred to vials on the plant stands. Greenhouse whiteflies of mixed age were collected from tobacco plants grown in the UBC greenhouse and were held for 2 h. Thirty unsexed whiteflies were released at the base of the plant stand. After 24 h, the number of adults settled and the number of eggs on each leaf was recorded.

The experiment was conducted as a completely randomized block design (RCBD). Fifteen cages were setup in the laboratory with each two choice treatment replicated five times on three alternate days (days=blocking factor) (total sample size = 15). The mean number of adults and eggs on excised leaves at 24 h was analyzed as a two-sample paired t-test with JMP (version 7.0.1). Model assumptions of equal variances and additivity between treatments were all verified.

4.2.2 No choice tests using whole plant in cage or excised leaf in container

Method 1 – Whole plant in cage cultivar comparison

Experiments were conducted as above in BugDorm2 cages (BioQuip Products, Inc.) in a windowless laboratory under fluorescent lights at UBC in January 2008 (Figure 4.2). Eight-week-old pepper seedlings were pruned immediately before the experiment so each plant had two leaves of approximately equal size and shape. The laboratory conditions were 23±2°C, 45% RH with a photoperiod of 12:12 (L:D). One whole plant of each cultivar (c.v., "Baselga", "Fascinato", "Orangery") was placed in the centre of each cage and a vial of whiteflies (n=30) was held upright at its base. After 24 h, the number of adults settled and eggs laid on each plant was recorded. The experiment was run three or four times per day and was replicated three times for a total number of 13 plants per cultivar. New plant material and insects were used for each sample.

A B

Figure 4.2. A) No choice pepper cultivar bioassay in cages. B) Individual pepper plant (c.v., "Fascinato") with vial of 30 adult whiteflies.

The mean numbers of adults and eggs per leaf of the whole plants were analyzed as a RCBD using analysis of variance in JMP (version 7.0.1). Days were random factors and the treatments were fixed factors. The model assumptions were verified. The residuals were normally distributed and centered about zero with constant variance.

Method 2 – Excised leaf in container cultivar comparison

Experiments were conducted in white, plastic 1 L containers (Figure 4.3) in a windowless laboratory under fluorescent lights at UBC in January 2008. Pepper leaves cut from the whole plants (see above) were placed in warm water. The leaves were gently washed and then transferred to small vials containing distilled water. A filter paper (Whatman® Number 2 [10 cm diameter]) was placed on the bottom of the container upon which the leaf + water + vial was placed. A vial containing 15 whiteflies was placed upright beside the water. Container lids were quickly secured to ensure no loss of whiteflies. The number of adults and the number of eggs per leaf were recorded after 24 h. The experiment was repeated five times per day and replicated three times for total number of 15 plants per cultivar.

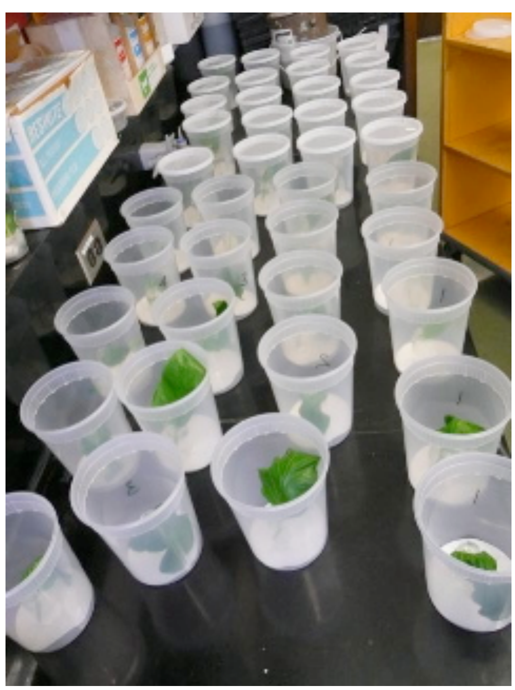

Figure 4.3. Excised pepper leaf cultivar comparison in 1 L plastic containers.

The mean numbers of adults and eggs per excised leaf were analyzed as a RCBD using analysis of variance in JMP (version 7.0.1). Days were random factors and the treatments were fixed factors. The model assumptions were verified. The residuals were normally distributed and centered about zero with constant variance.

4.3 Results

4.3.1 Two choice tests with excised pepper leaves

Results from the two choice tests revealed no significant differences in adult settling and oviposition between the three pepper cultivars (Figures 4.4 and 5.5). This indicates that adult whiteflies did not demonstrate any preferences between the three pepper cultivars tested.

4.3.2 No choice tests using whole plant in cage or excised leaf in container

Method 1 – Whole plant in cage cultivar comparison

Results from the no choice tests comparing adult settling and oviposition on whole plants revealed no significant differences between the three pepper cultivars (Table 4.1). This indicates that in a no choice setting, adult settling and oviposition was relatively equal on all whole pepper plants.

Method 2 – Excised leaf in container cultivar comparison

No choice tests using excised pepper leaves in small closed containers showed no significant differences between adult settling and oviposition on the three pepper cultivars (Table 4.1).

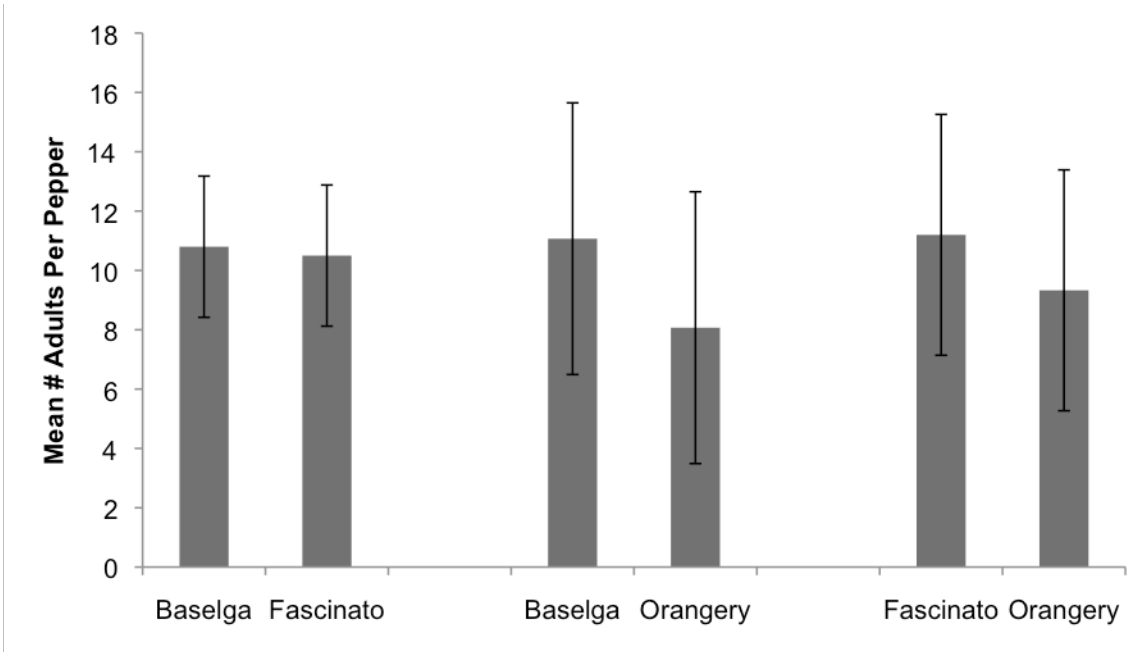

Figure 4.4. Experiment 4.2.1. Mean (±2SEM) number of adults settled per pepper leaf on each cultivar in two choice tests. An overlap of the error bars indicates no significant difference between means (p≤0.05).

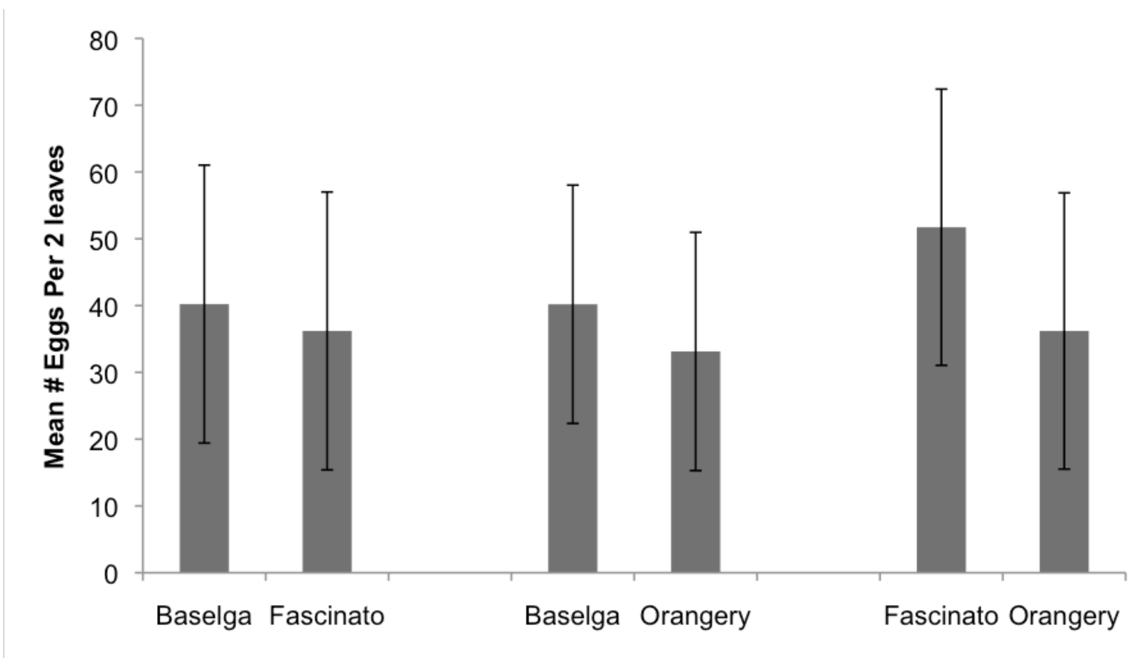

Figure 4.5. Experiment 4.2.1. Mean (±2SEM) number of eggs per pepper leaf on each cultivar. An overlap of the error bars indicates no significant difference between means (p≤0.05).

Table 4.1. ANOVA analysis of the mean (±2SEM) number of adults and the mean number of eggs per pepper leaf at 24 h on whole plants and excised leaves.

	Whole Plant		Eggs	
	Adults/leaf	**Eggs/leaf**	**Adults/leaf**	**Eggs/leaf**
Baselga	4.44±0.9	27.85±10.7	6.17±2.18	22.58±10.84
Fascinato	3.44±0.9	26.00±10.7	6.58±2.18	15.58±10.84
Orangery	3.90±0.9	29.23±10.7	5.58±2.18	17.92±10.84
***F* and *p* values**	$F(2,35)=1.93$ $p=0.1596$	$F(2,35)=0.41$ $p=0.6659$	$F(2,30)=0.39$ $p=0.6816$	$F(2,30)=0.82$ $p=0.4511$

4.4 Discussion

Laboratory bioassays were conducted to determine if *T. vaporariorum* settling and oviposition behaviours after 24 h were significantly modified by commercial sweet pepper cultivars (c.v., “Baselga”, “Fascinato” and “Orangery”). Results from the two choice tests and the no choice tests indicated that *T. vaporariorum* did not prefer to settle or oviposit on any pepper cultivar tested. Therefore, it was concluded that the selected pepper cultivars were not significant modifiers of whitefly settling and oviposition behaviours. A lack of differences between whitefly settling and oviposition on the commercial cultivars tested was attributed to the narrow range of plant material compared and broader comparison evaluating more cultivars is recommended.

In a review of plant resistance to whiteflies, De Ponti *et al.* (1990) state that ‘a careful search for resistance will always be rewarded’. Based on this statement, I attempted to demonstrate whitefly preferences between pepper cultivars using a variety of bioassay techniques. However, my thesis objective was to evaluate plant resistance to whiteflies as a potential modifier of its behaviour in the context of other control tactics. Therefore, I concluded that whitefly behaviour was not significantly affected by the pepper cultivars that I tested and further evaluation of plant resistance in combination with other tactics was not pursued.

The results of the whole plant versus excised leaf no choice tests suggested more adults settled on peppers in the excised leaf-container bioassay than the whole plant-cage bioassay. For each assay type, whiteflies were released at a rate of 15/leaf. The whole plant-cage assays were conducted in cages which were much larger than the 1 L container used for the excised leaf assay. With respect to time and supplies required, the excised leaf assay is a more efficient method of evaluating whitefly settling. The 1 L containers provide less space for whiteflies to disperse and more adults per leaf would be expected. Although more adults settled per leaf in the container assay, oviposition was significantly higher on whole plants than on excised leaves. Reduced oviposition on excised leaves has been previously demonstrated for excised tomato leaves (Noldus *et al.*, 1986). Based on these results with excised leaves and previous reports of problems associated with excised leaves, the use of whole plants was adopted for subsequent experiments (see Chapter 5).

Although sweet pepper is considered to be a low-ranked host for *T. vaporariorum,* large differences in pepper resistance to whiteflies were previously found for commercial sweet pepper cultivars from western and central Europe (Laska *et al.*, 1982; van Lenteren *et al.*, 1989; De Ponti *et al.*, 1990). Based on comparisons between peppers from western and central Europe, the researchers found that cultivar traits affected both whitefly preferences and performances. In a different study with *T. vaporariorum,* researchers found that the location of plant resistant factors depended up the plant species being studied (Lei *et al.*, 1999). In peppers, resistance factors were found on the leaf surface and in the mesophyll. In tomatoes, resistance factors appeared to be present in the phloem tissue. Numerous studies evaluating plant resistance to *B. tabaci* and *T. vaporariorum* have explored the effects of leaf surface topography and trichomes on whitefly plant resistance in cotton, tomato (De Ponti *et al.*, 1990). In general, the effect of trichomes or leaf surface exudates on plant resistance to whiteflies depends upon the plant species.

In conclusion, insect resistant cultivars are said to improve crop defense leading to improved plant yields and reduced pesticide use (Smith, 1989). Furthermore, plant resistance is considered to be highly compatible with other alternative pest control tactics such as trap cropping, biological controls and cultural controls (De Ponti *et al.*, 1990; Hokkanen, 1991). Plant resistance is often attributed to three mechanisms (antibiosis, antixenosis and tolerance). In general, most plant resistance studies test either antibiosis or antixenosis. Plant tolerance to whiteflies is rarely reported. Previous reports of whitefly plant resistance demonstrate its potential as a whitefly management tool. However, additional work is needed to overcome the challenges of testing plant resistance and the identification of resistant pepper strains would be required for breeding programs.

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Chapter 5[*] Combining trap crops and yellow sticky traps with Safer's Soap for greenhouse whitefly (*Trialeurodes vaporariorum)* management on sweet peppers (*Capsicum annuum)*

5.1 Introduction

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), is a major pest of greenhouse grown tomato, pepper, cucumber, and eggplant as well as numerous ornamental species (Ferguson *et al.*, 2003; AAFC, 2005). Whiteflies reduce plant vigor and crop quality by removing phloem, excreting honeydew (which fosters the growth of sooty mould *Cladosporium*) and by transmitting plant viruses (Lloyd, 1922). A variety of factors including whitefly resistance to pesticides, increasing costs of pesticides, governmental restrictions on pesticide use and a lack of chemicals appropriate for biological control, have led to grower interest in alternative whitefly management tactics (British Columbia Greenhouse Growers' Association, personal communication). Alternative pest controls (i.e. biological controls, pheromones, plant extracts, trap crops and yellow sticky traps), when employed alone, often provide ineffective control of the target pest and cannot compete against broad-spectrum pesticides. Agricultural entomologists recommend combining alternative methods into integrated management strategies to improve pest management (Pickett *et al.*, 1997; Moreau *et al.*, 2006). The push-pull strategy is an example of a coordinated management strategy involving the behavioural manipulation of insect pests. Push-pull proposes the use of combinations of putative repellents and attractive stimuli to direct the movement of insects away from protect resources. Economic crops are protected from pests, by repellent plants, antifeedants, or oviposition deterrents. At the same time, pests are localized on trap crops, using aggregative semiochemicals and attractants, so that a selective control agent (biological control) can be used to reduce pest populations (Cook *et al.*, 2007).

In earlier thesis chapters, the effects of trap crops, yellow sticky traps, plant extracts and oils, insecticidal soaps and plant resistance were individually tested as

[*]A version of this chapter will be submitted for publication. Moreau, T.L. and M.B. Isman. 2010. Combining trap crops and yellow cards with Safer's Soap for whitefly management on sweet peppers.

whitefly control tactics. Eggplant trap crops, Safer's Natural Insecticide (Safer's Soap) and yellow sticky traps were selected to test in combination strategies because of their behaviour modifying properties and suitability for immediate use in commercial greenhouses.

The objective of this experiment was to evaluate how combinations of alternative control tactics affected *T. vaporariorum* settling and oviposition on pepper crops and traps. More specifically, the goal was to determine if whitefly control efficacy of trap crops, yellow sticky traps and Safer's Soap was increased through simultaneous deployment of these methods. The following questions provided the framework from which this experiment was developed and conducted:

1. How much do trap crops and settling deterrents reduce whitefly settling and oviposition on main crops?
2. Does supplementing trap crops with additional visual cues increase the number of whiteflies trapped?
3. Can whitefly densities on crops be reduced through combinations of alternative controls? If so, which combinations are most effective at reducing densities on pepper crops?

5.2 Materials and Methods

The influence of trap crops, yellow sticky traps and Safer's Soap on the settling and oviposition behaviour of adult whiteflies was evaluated in May 2008. Experiments were conducted in BioQuip® Bugdorm-2 cages in a windowless laboratory at the University of British Columbia (UBC) under fluorescent lights. Room conditions were approximately 23±2°C, 45% RH with a photoperiod of 12:12 (L:D). The main crop, represented by four sweet pepper seedlings (c.v., "Forever", Enza Zaden), was placed in a square (25 cm between peppers on the corners) within the cage. Trap crops were placed in the centre of the square (Figure 5.1). At the beginning of the trial, 60 adult whiteflies were released from two plastic vials at the sides of the cage. Counts of whiteflies on main crops and trap crops were taken after 24 h.

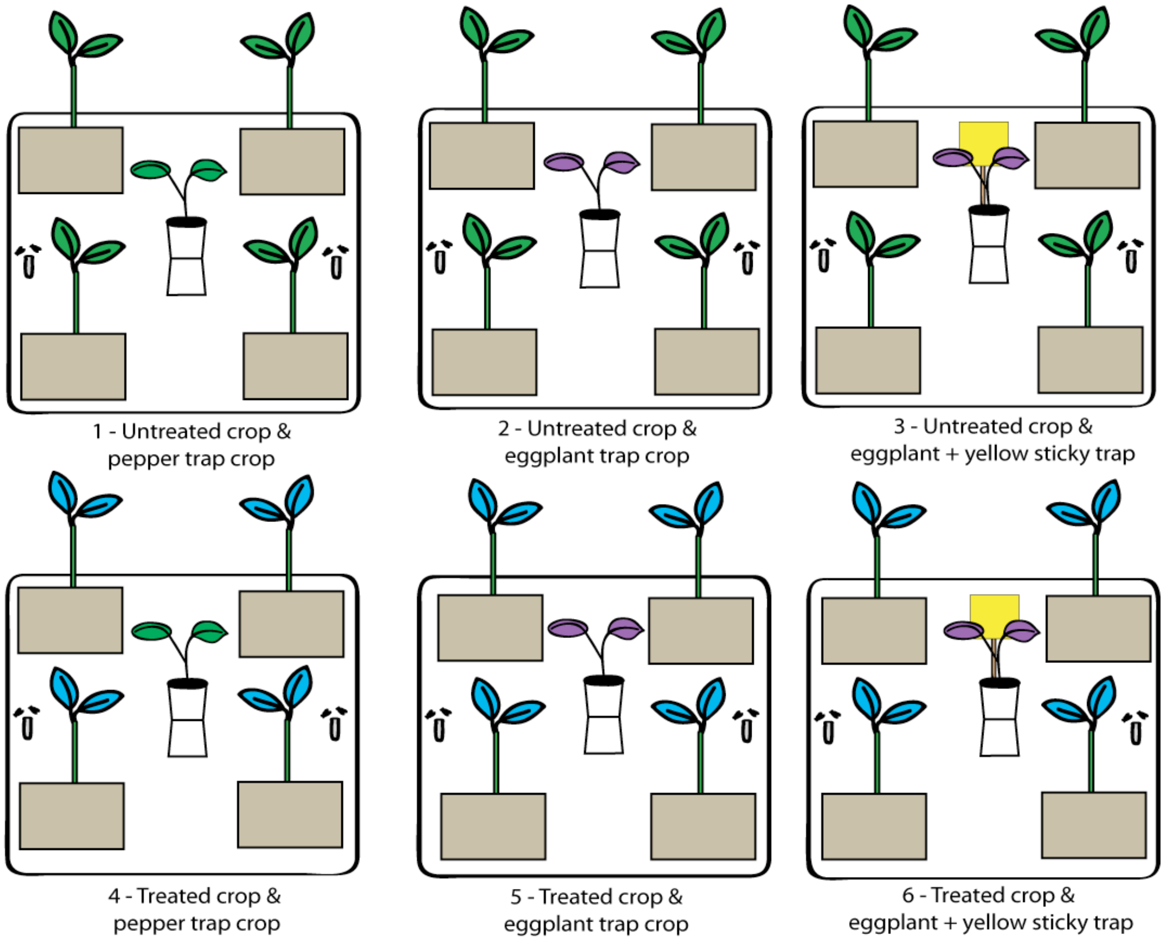

Figure 5.1. Experimental design of six treatment combinations evaluating two spray treatments (untreated crop versus treated crop [5% Safer's Soap]) and three trap treatments (pepper [control], eggplant, eggplant + yellow sticky trap) on whitefly settling on main crops and trap crops.

The experiment was a 2x3 factorial randomized complete block design (RCBD). There were two spray treatments on the main crop (untreated crop and treated crop [5% Safer's Soap]) and three trap treatments (pepper [control], eggplant, and eggplant + yellow sticky trap). The six treatment combinations evaluated were: (1) untreated crop & pepper trap; (2) untreated crop & eggplant trap; (3) untreated crop & eggplant + yellow sticky trap; (4) treated crop & pepper trap; (5) treated crop & eggplant trap; and (6) treated crop & eggplant + yellow sticky trap (Figure 5.1). Treatments were randomly assigned to six cages. Each group of six treatments was replicated three or four times per 24 h. The experiment was replicated on alternate 24 h periods (blocking factor = 24 h period). The number of samples for each treatment combination was 15.

Pepper seedlings were obtained from Houweling Nurseries (Delta, BC) at an age of four weeks. Plants were moved to the Horticulture Greenhouse at UBC and grown under natural daylight conditions. Plants were irrigated and fertilized daily with a dilute fertilizer solution of 100 ppm of 15-5-15 Cal-Mag (Scotts, Peters Excel). When pepper seedlings were six weeks old they were pruned to have two leaves of similar size and age. Eggplants (c.v., “Dusky”) were 8 weeks old and plants were pruned to two leaves. All experimental plants were used one day after pruning. A 5% concentration of Safer’s Soap in distilled water was applied to randomly selected pepper plants. Treated plants were sprayed with 6 ml of solution using a hand-help sprayer. Untreated pepper crops were sprayed with 6 ml of distilled water. All plants were air dried for 30 minutes. In Chapter 2, the stickiness of the yellow sticky traps was considered an unfair advantage when comparing yellow sticky traps to trap crops. Therefore, for this experiment, stickiness of yellow sticky traps was removed by covering each 100 cm^2 trap in clear cellophane.

Trialeurodes vaporariorum were collected from a natural population established in the UBC Greenhouse. Adults of mixed age and sex were aspirated from tobacco (*Nicotiana sp.)* plants approximately two hours before the start of the experiment. 60 unsexed whiteflies were released from two plastic vials (30 adults/vial) at the sides of each cage. An additional ten vials (30 wfs/vial) of adults were collected each day of the trial (days = 4) to determine the sex ratio of the released adults. After the vials were opened in the cages, whiteflies were allowed to leave without further disturbance. Twenty-four hours after whitefly release, the numbers of adults settled on the four crops and on one trap plant were recorded and all the adults were collected to determine the number of males and females on each plant. The numbers of eggs per crop and per trap were counted using a dissecting microscope.

The average number of adults (# females, # males and total) and the average number of eggs per crop (average of 4 plants) and trap were separately analyzed in a 2-way ANOVA as a 2x3 factorial design. Means are presented plus or minus 2 standard errors of the mean (±2SEM). Total numbers of recovered whiteflies per cage was analyzed using the same design. All analyses were conducted in JMP (version 7.0.1) with the Fit Model Platform. Day and cage were random factors and the treatments were fixed factors. The Tukey-Kramer post-hoc test was used to determine which treatment level means were statistically different from each other. Model assumptions were tested for each ANOVA. If the residuals were not normally distributed, or centered about zero with constant variance the data was transformed (log10). If outliers were identified, models were run with and without outliers to compare outputs. An outlier was identified in the crop female, crop male, trap male and total recovered data and was therefore removed from the analysis.

5.3 Results

5.3.1 Adult total densities on main crops and trap crops

Comparison of total adult settling per main crop revealed no significant interaction between the spray treatment and trap treatment ($F_{2,76}$=0.17, p=0.84) (Table 5.1). Both main effects of spray treatment and trap treatment were found to be significant ($F_{1,78}$=5.549, p=0.0216) and ($F_{2,77}$=37.7, p=0.0001) respectively. Tukey-Kramer post-hoc tests demonstrated that more adults settled on crops that were not sprayed with Safer's Soap compared to crops that were sprayed (Figure 5.2). For the main effect of trap treatment, Tukey-Kramer post-hoc tests showed that main crops in the control (pepper) trap treatment had significantly more adults per plant than the eggplant treatment and the eggplant + yellow sticky trap treatment. Combining eggplants with yellow sticky traps significantly decreased the number of adults settling on crops compared to eggplant alone.

Comparisons of total adult settling on traps revealed no significant interaction between the main effects ($F_{2,76}$=1.23, p=0.2971) and no significant effect of spray treatment ($F_{1,77}$=2.83, p=0.0963) (Table 5.2). Trap treatments significantly affected the number adults per trap ($F_{2,77}$=50.71, p=0.0001) (Figure 5.3). Significantly more adults were found on traps in the eggplant + yellow sticky trap treatment and the eggplant treatment than in the control (pepper) treatment (Figure 5.3). There were no significant differences between the number of adults trapped on eggplant alone and eggplant combined with a yellow sticky trap.

5.3.2 Male and female densities on main crops and trap crops

For each day of the experiment, an additional 10 vials of whiteflies (30 adults/vial) were collected to determine an estimate of the sample population sex ratio. The average number of males and females per vial was 7.5 and 22 respectively. This equates to an approximate ratio of 1 male to 2.9 females. The average sex ratio was 1:3.7 (male:female) on crops and 1:2.7 on traps. Female and male densities on crops and traps revealed no significant interactions between the main effects (Table 5.1 and 5.2). The effect of spray treatment on the density of males on crops was marginally significant ($F_{1,77}$=4.12, p=0.0458) but there was no significant effects of spray on male densities on traps ($F_{1,75}$=0.12, p=0.7337). Spray treatment significantly reduced female crop densities ($F_{1,76}$=7.59, p=0.0073) while increasing female trap densities ($F_{1,77}$=4.61, p=0.0348) (Figure 5.3). There was no effect of spray treatment on total adult trap densities ($F_{1,77}$=2.83, p=0.0963).

Trap treatments significantly affected female and male densities on crops and traps (Table 5.1 and 5.2). Female settling on crops was lowest in the eggplant + yellow sticky trap treatment (Figure 5.3). Yellow sticky traps combined with eggplants significantly reduced female settling on crops compared to eggplant alone. Male settling on crops was reduced by eggplant and eggplant + yellow sticky traps compared to the pepper trap (control). However, no significant difference between the eggplant and the eggplant + yellow sticky trap treatments on male densities was found. Adult settling of males, females and total whiteflies on traps showed significantly more whiteflies settled on eggplant and eggplant + yellow sticky traps than on pepper traps. There was no significant difference between whitefly settling on eggplant and eggplant + yellow traps.

5.3.3 Egg densities on main crops and trap crops

Results of whitefly oviposition on crops revealed no significant interaction between the spray treatment and the trap treatment ($F_{2,67}$=0.05, p=0.9491) (Table 5.1). Investigation of the main effects found no significant effect of spray treatment on whitefly oviposition ($F_{1,68}$=1.98, p=0.1640). There was a significant effect of trap treatment on the mean number of eggs per main crop ($F_{2,64}$=14.61, p=0.0001). Tukey-

Kramer post-hoc analysis revealed a significant difference in the number of eggs on crops for all trap treatments (Figure 5.4). Crops in the eggplant + yellow treatment had the fewest eggs, followed by crops in the eggplant treatment and the pepper treatment.

No significant interaction between the spray treatment and trap treatment on whitefly oviposition on traps was found ($F_{2,75}$=1.89, p=0.1587), nor was the main effect of spray treatment significant ($F_{1,76}$=2.69, p=0.1050) (Table 5.2). There was a significant effect of trap treatment on whitefly oviposition on traps ($F_{2,74}$=24.67, p=0.0001). Tukey-Kramer post-hoc tests showed significant increases in the number of eggs per trap in the eggplant and eggplant + yellow trap compared to the pepper trap (Figure 5.4). No significant differences between whitefly oviposition on eggplant or eggplant + yellow trap treatments were found.

5.3.4 Adult Recovery

Sixty adult whiteflies were released in each cage at the beginning of the experiment. The 2-way ANOVA indicated no significant interaction between spray treatment and trap treatment on the number of whiteflies recovered ($F_{2,68}$=2.85, p=0.0648) (Table 5.2). Spray treatments had no significant main effects on whitefly recovery ($F_{1,68}$=0.19, p=0.6603). There was a significant effect of trap treatment on whitefly recovery ($F_{2,70}$=9.82, p<0.0002). Tukey-Kramer post-hoc tests showed a significant increase in the number of whiteflies recovered in treatments with traps than in treatments without traps.

Table 5.1. The mean (±2SEM) number of *T. vaporariorum* adults (females, males and total) and eggs per MAIN CROP, 24 h after releasing 60 adults/cage. N=15

		Adults			
Crop Treatment	***Trap Treatment***	***Females***	***Males***	***Total***	***Eggs***
Untreated Crop	Pepper Trap	6.23±0.9	1.67±0.4	8.46±1.2	56.45±11.9
	Eggplant trap	4.63±0.9	1.19±0.4	6.01±1.2	37.54±11.9
	Eggplant + yellow trap	3.24±0.9	0.99±0.4	4.32±1.2	25.3±11.9
Treated Crop	Pepper Trap	5.44±0.9	1.34±0.4	7.82±1.2	47.45±11.9
	Eggplant trap	3.65±0.9	0.97±0.4	4.80±1.2	34.54±11.6
	Eggplant + yellow trap	2.41±0.9	0.69±0.4	3.28±1.2	20.44±11.9
	Crop Spray	$F(1,76)=7.6$ $p<0.0073$**	$F(1,77)=4.1$ $p=0.0458$	$F(1,78)=5.5$ $p<0.0216$*	$F(1,70)=2.0$ $p=0.1640$
	Trap	$F(2,75)=30.4$ $p<0.0001$**	$F(2,77)=7.3$ $p<0.0012$**	$F(2,77)=37.7$ $p<0.0001$**	$F(2,66)=14.6$ $p<0.0001$**
	*Crop spray*trap*	$F(2,76)=0.03$ $p=0.9669$	$F(2,75)=0.06$ $p=0.9450$	$F(2,76)=0.17$ $p=0.8409$	$F(2,69)=0.05$ $p=0.9491$

* indicates a significant difference at p < 0.05, ** indicates a significant difference at p < 0.01

Table 5.2. The mean (±2SEM) number of *T. vaporariorum* adults (females, males and total) and eggs per *TRAP,* 24 h after releasing 60 adults/cage. N=15

		Adults				
Crop Treatment	***Trap Treatment***	***Females***	***Males***	***Total***	***Eggs***	***Total # Adults Recovered Per Cage***
Untreated Crop	Pepper Trap	7.35±4.4	3.61±2.2	11.62±5.0	81.97±56.6	45.85±4.5
	Eggplant trap	17.22±4.4	7.48±2.2	26.21±5.0	137.97±56.6	49.13±4.5
	Eggplant + yellow trap	21.95±4.4	6.68±2.2	31.43±5.0	189.97±56.6	49.55±4.5
Treated Crop	Pepper Trap	7.98±4.4	2.94±2.2	11.15±5.0	98.51±56.6	43.71±4.5
	Eggplant trap	23.15±4.4	8.18±2.2	32.92±5.2	201.04±56.2	52.35±4.5
	Eggplant + yellow trap	23.91±4.4	7.46±2.2	34.65±5.0	214.71±56.6	47.06±4.5
	Crop Spray	$F(1,77)=4.6$ $p<0.0348$*	$F(1,75)=0.12$ $p=0.7337$	$F(1,77)=2.83$ $p=0.0963$	$F(1,76)=2.7$ $p=0.1050$	$F(1,69)=0.19$ $p=0.6603$
	Trap	$F(2,77)=50.0$ $p<0.0001$**	$F(2,73)=12.5$ $p<0.0001$**	$F(2,77)=50.7$ $p<0.0001$**	$F(2,74)=24.7$ $p<0.0001$**	$F(2,70)=9.8$ $p<0.0002$**
	*Crop spray*trap*	$F(2,76)=1.5$ $p=0.2214$	$F(2,74)=0.35$ $p=0.7088$	$F(2,76)=1.23$ $p=0.2971$	$F(2,75)=1.9$ $p=0.1587$	$F(2,68)=2.6$ $p=0.0648$

* indicates a significant difference at $p < 0.05$, ** indicates a significant difference at $p < 0.01$

Figure 5.2. Main effects of SPRAY treatment (untreated crop and treated crop [5% Safer's Soap) on the mean (±2SEM) number of ADULTS settling (females, males and total) on crops and traps. Asterix ** above bars indicates a significant difference between the two treatments (p < 0.05).

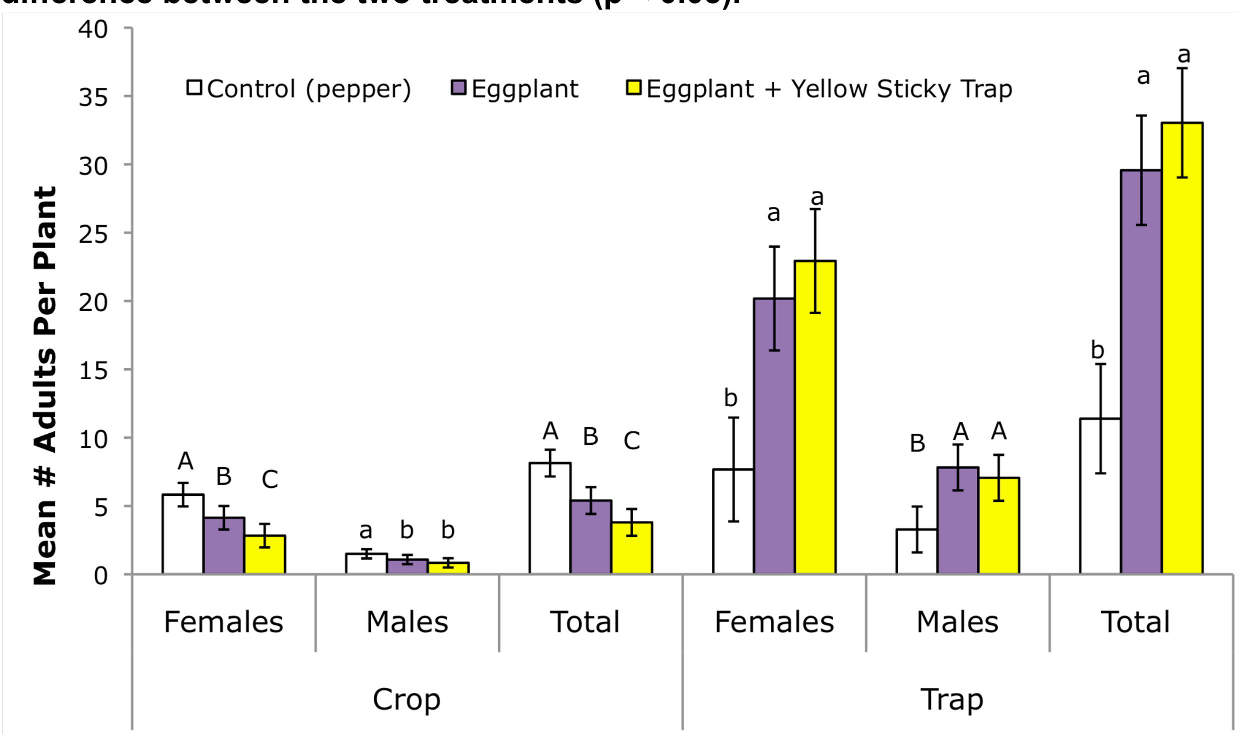

Figure 5.3. Main effects of TRAP treatments (control [pepper], eggplant, eggplant + yellow sticky car) on the mean (±2SEM) number of ADULTS settling (females, males and total) on crops and traps. Means with the same lower and upper case letters are not significantly different (p < 0.05).

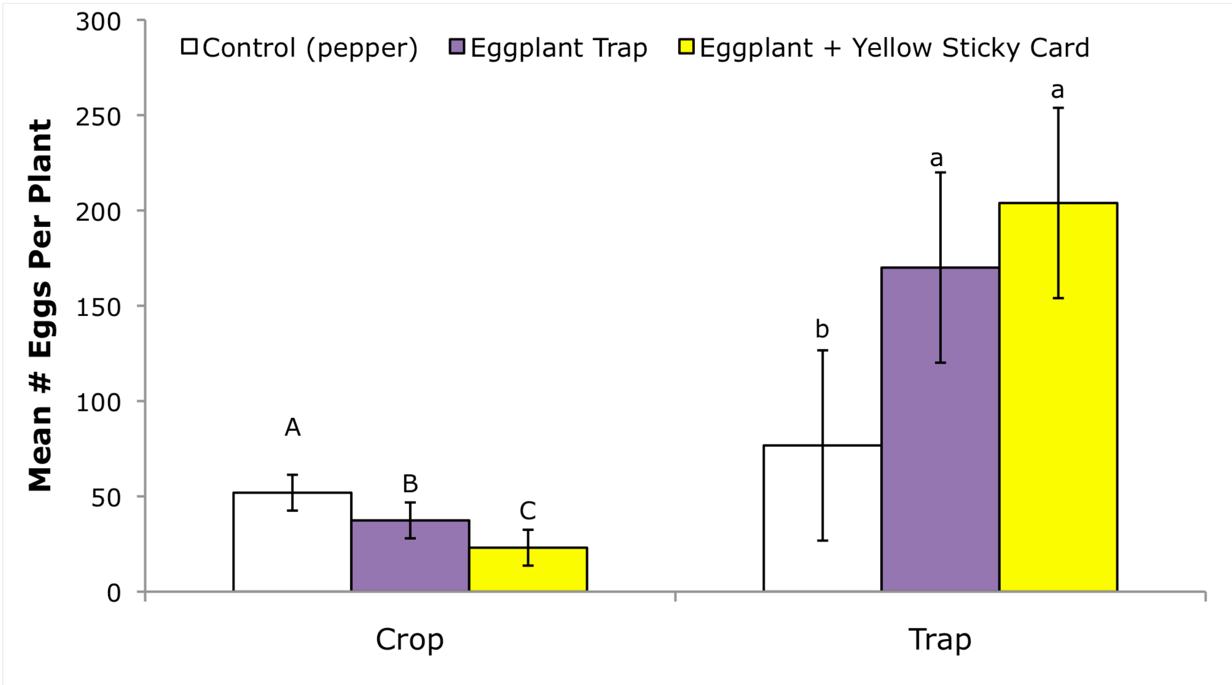

Figure 5.4. Main effects of TRAP treatment (control [pepper], eggplant, eggplant + yellow sticky trap) on the mean (±2SEM) number of EGGS on crops and traps. Means with the same lower and upper case letters for crops and traps are not significantly different ($p < 0.05$).

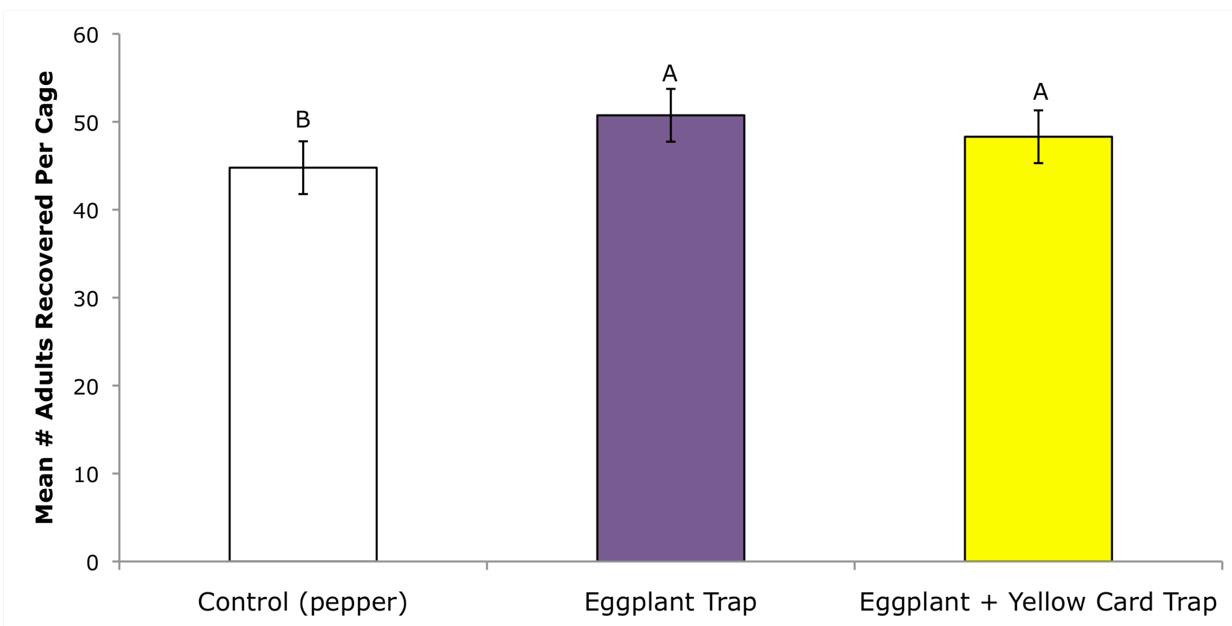

Figure 5.5. Main effects of TRAP treatment (pepper [control], eggplant, eggplant + yellow sticky trap) on the mean (±2SEM) number of ADULTS RECOVERED PER CAGE. Means with the same upper case letter are not significantly different ($p < 0.05$).

5.4 Discussion

Greenhouses have been suggested as ideal sites for trap crop management given the contained space and controlled environment (Buitenhuis & Shipp, 2006). The results of these combination trials with *T. vaporariorum* indicated that the lowest adult densities on main crops were obtained when all three tactics were used. However, the 3-way combination of eggplant, yellow sticky trap and 5% Safer's Soap was not significantly different than 2-way combination of eggplant plus yellow trap**.** Therefore, combining traps with sprays did not significantly reduce whitefly settling and oviposition on peppers. No interaction effects between the spray and trap treatments were found for any whitefly response measured (females, males, total adults and eggs) further indicating that there was no advantage to combining trap treatments with a Safer's Soap spray. An evaluation of the main effects of trap and spray treatments found trap treatment significantly affected whitefly settling and oviposition on both main crops and traps. The main effect of spray treatment showed fewer effects on adult settling and no effects on whitefly oviposition on main crops and traps.

Eggplant, when used alone as a trap crop, significantly reduced the number of adult whiteflies on main crops by 34% compared to the control. When eggplants were combined with yellow traps, the number of adults on main crops was reduced by 53%. Therefore, adding a yellow trap to eggplant provided additional reductions of adults on main crops. The effect of traps on whitefly oviposition on main crops found that compared to the control (pepper), eggplant reduced the number of eggs per main crop by 28% and eggplant + yellow sticky trap reduced the number of eggs per main crop by 56%. These results support the hypothesis that trap crops and combinations of trap crops with other tactics reduce *T. vaporariorum* populations on peppers.

Results from Chapter 3 suggested that a 2% Safer's Soap application to pepper disks reduced adult settling by 23% compared to the control but did not significantly reduce whitefly oviposition on treated disks. Similarly, the results of this current experiment found that a 5% Safer's Soap application reduced adult settling by 15% but did not significantly reduce oviposition. An explanation for a lack of significance of

Safer's Soap on whitefly oviposition may have resulted from higher variability obtained with oviposition data compared to the adult data. Furthermore, 5% Safer's Soap is a low dosage and an increased concentration may be more effective for reducing adult settling and oviposition on peppers.

Previous reports of gender-specific responses during whitefly host selection are scarce. Pheromones usually elicit responses only in male insects, whereas host plant chemicals are thought to mainly affect females (Finch, 1980). In contrast, Li and Maschwitz (1983) reported the discovery of a female *T. vaporariorum* pheromone that was found to attract males within a short distance. However, since this discovery very little follow-up of whitefly pheromones has been published. Whitefly female to male sex ratios are often reported as being 1:1 with the knowledge that the ratio changes throughout the year (Byrne & Bellows, 1991). The results of this study with *T. vaporariorum* demonstrated that the sex ratio of the sample population was 1:2.9 (male: female). Evaluation of the effects of Safer's Soap on male and female whiteflies indicated female settling behaviour might be more affected by the soap treatment than males. Increased sensitivity of females to host plant cues would provide an adaptive advantage for her offspring. Oviposition site selection is very important for whitefly survival due to the sessile nature of the nymphs and *T. vaporariorum's* oviposition choices have been shown to correlate to host suitability for offspring (van Lenteren & Noldus, 1990). For whitefly pest management, modifying the behaviour of dispersing females could be an effective means of reducing oviposition on crops. Further study of male and female responses is necessary to improve our understanding of gender-specific behaviours associations with specific environmental cues.

Trap crops significantly affected the total number of whiteflies recovered per cage. More adults were recovered per cage in the eggplant and eggplant + yellow sticky trap treatment than in control (pepper) treatments. The fate of the unrecovered whiteflies was not known but adult settling on cages (data not shown) was compared and no differences between treatments were found. Unrecovered whiteflies were presumed to have died. Although, sweet peppers are considered low-ranking *T. vaporariorum* hosts compared to other plant species such as eggplant and cucumber, whiteflies do become pepper pests in commercial settings (van Lenteren & Noldus, 1990). Whitefly host plant induction has been previously demonstrated following long-time associations with plant species (Lei *et al.*, 1998). However, previous studies with *B. tabaci* report decreased whitefly survival when no high-ranking hosts were present (Bird & Kruger, 2006). Naturally established populations of *T. vaporariorum* used in this current experiment were collected from a high-ranking host, tobacco. Therefore, higher mortality in pepper cages could have resulted from a lack of high-ranking hosts. Recently, Lee *et al.* 2009 demonstrated whitefly mortality on main crops was an unexpected factor influencing trap crop effectiveness in poinsettia crops. Through simulation studies, these authors found that low whitefly mortality on main crops was a requisite for preferred plants to act as trap crops. This implies that in less-preferred crops a proportion of whiteflies would naturally die off. However, if a preferred host is present, in the form of a trap crop, whitefly mortality may be reduced. Therefore, additional studies of whitefly population dynamics over time are necessary.

Commercial application of *T. vaporariorum* trap crops in poinsettia greenhouses has shown that trap crops integrate well with biological control programs (Murphy *et al.*, 2006). Within a greenhouse, whitefly movement is influenced by many factors including host plant quality, solar radiation, temperature, and wind speed (Blackmer & Byrne, 1993; Riis & Nachman, 2006). On gerbera and tomato plants, whiteflies movement was observed at an average speed of 3 cm per hour and travel on average 105 cm over 3.5 days (Noldus *et al.*, 1986; Sutterlin, 2000). Pest monitoring within commercial sweet pepper greenhouses is difficult because crops are very dense and can grow from 12 to 15 feet tall. For growers, concentrating whiteflies at a predetermined site within greenhouses could improve pest control by decreasing the amount of biological or chemical controls required.

In conclusion, these results demonstrated eggplant trap crops combined with yellow sticky traps reduced adult and egg densities on crops by 53% and 56% respectively. Whitefly reduction was somewhat enhanced by crop treatment with Safer's Soap but not enough to justify the expense and time. The targeted use of trap crops and visual traps at whitefly entry points within commercial pepper greenhouses may improve whitefly monitoring and control. From a practical standpoint, trap crop management requires growers to maintain healthy trap plants. Traps with whiteflies must be removed or managed to prevent whitefly movement from traps to crops. In future studies, the efficacy of traps at time internals longer than 24 h should be addressed. Furthermore, additional information about the density of traps within greenhouses, their combination with other tactics and trap enhancement with visual cues is required.

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Chapter 6: Conclusions

From January 2006 through May 2009, a series of experiments were conducted in Vancouver, British Columbia at the University of British Columbia (UBC). The three main areas of study explored in this thesis were alternative pest management techniques, insect host selection and insect behavioural manipulation of whiteflies on greenhouse-grown sweet peppers. Whitefly host selection within commercial greenhouses inevitably affects pest control. However, whitefly host finding over long-distances and host acceptance over short-distances is complex and depends on a variety of abiotic conditions and biotic factors (Chapter 1). The primary objective of this project was to determine which alternative pest control tactics, trap crops (TCs), yellow sticky traps (YSTs), reduced-risk sprays (RRSs) and plant resistance (PR), were the greatest modifiers of whitefly settling and oviposition behaviours on sweet peppers. The secondary objective was to determine if combining tactics increased whitefly suppression on sweet peppers through simultaneous application of behavioural manipulators.

Results of individual tactics tested in Chapters 2 – 4 indicated the greatest modifiers of *T. vaporariorum* settling and oviposition behaviours were YSTs > TCs > RRSs > PR. By combining control tactics in Chapter 5, whitefly settling was lowest on sweet peppers in the trap crops + yellow sticky trap + reduced-risk spray treatment. However, there was no significant benefit of the 3-way combination over the 2-way combination of trap crop + yellow sticky trap. Furthermore, reduced-risk spray treatment was moderately effective at reducing whitefly settling on peppers, but was not effective at reducing whitefly oviposition. The use of traps provided a more consistent and effective method to reduce adult and egg densities on peppers than reduced-risk sprays. Based on my current understanding of *T. vaporariorum* host selection, I suspect the sensory abilities affected by these tactics are: yellow sticky traps – vision; trap crops – mechanoreception and chemoreception (mainly gustation but perhaps olfaction); reduced-risk sprays – chemoreception and mechanoreception; and plant resistance – chemoreception and mechanoreception (Figure 6.1).

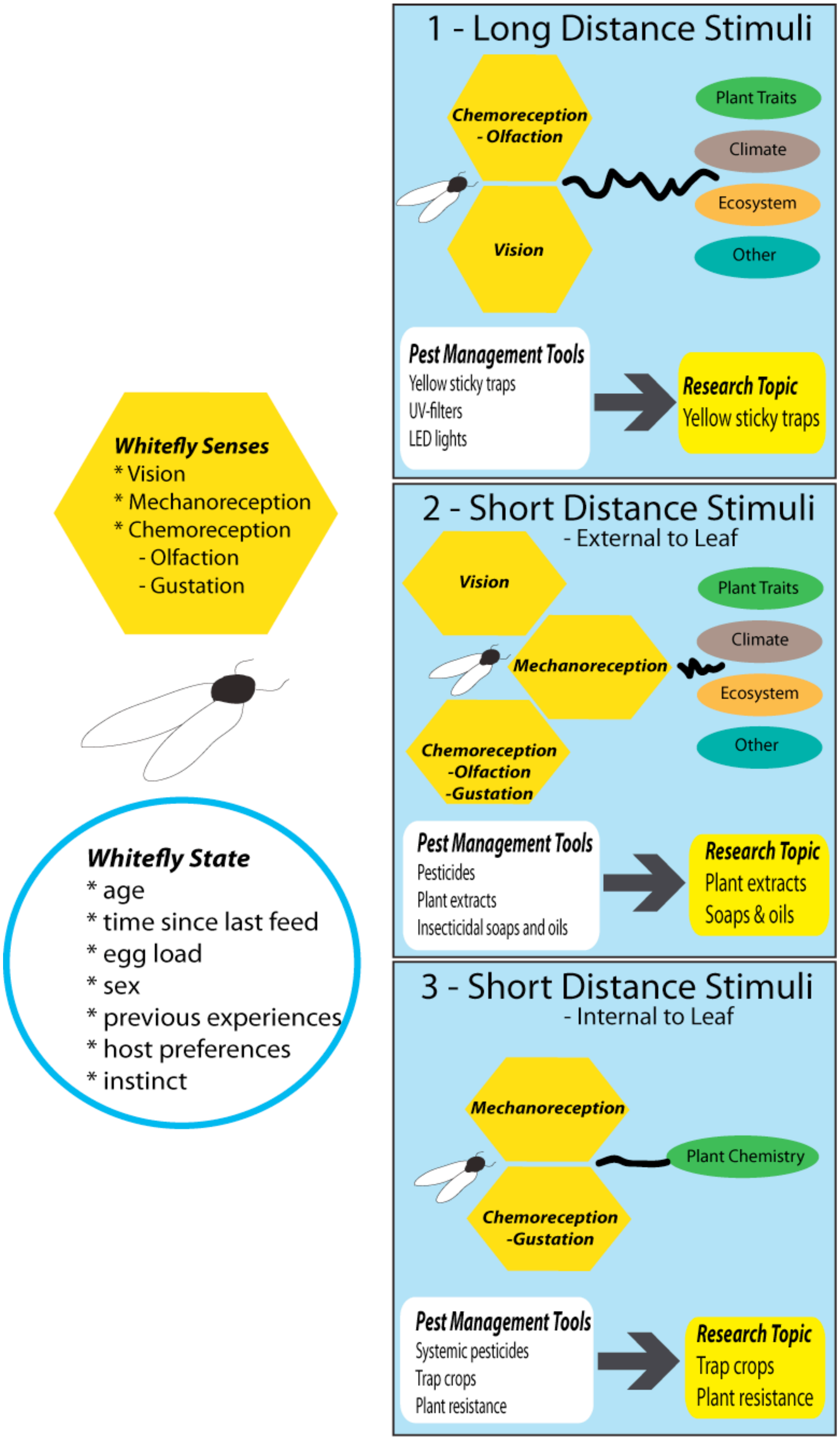

Figure 6.1. An overview of whitefly host selection and the factors that may influence its behaviour over long- and short-distances.

Results of chapter 2 indicated yellow sticky traps were more effective adult traps than eggplant and squash trap crops. However, due to large variability in the data, yellow sticky traps did not significantly reduce adult settling on peppers but they did reduce oviposition by 59%. Whitefly attraction to the yellow sticky traps supports previous work that indicates *T. vaporariorum* long-distance host finding is mediated largely by whitefly responses to visual cues (Vaishampayan *et al.*, 1975; Gillespie & Quiring, 1987; van Lenteren & Noldus, 1990). In Chapter 5, the addition of yellow sticky traps to a trap crop significantly reduced adult and egg densities on pepper compared to eggplant alone. For generalist feeding insects, a reduction in the number and complexity of cues used in food choice is thought to clarify the differences between foods and nonfoods (Bernays, 1996). For many animals, when more attention is paid to the inputs of one sense (e.g. vision), subsequently less attention is paid to cues associated with other senses (e.g. olfaction) (Roitblat, 1987). For whiteflies, responses to long-distance visual cues were found to trigger the most consistent modification to whitefly settling behaviours. Although yellow sticky traps are used as monitoring tools, additional use of whitefly visual traps with trap crops would likely enhance whitefly trap crop efficacy. For future studies, whitefly visual responses to other cues such as light-emitting diodes, UV reflecting traps, or different shaped traps, is recommended (Antignus *et al.*, 2001; Chu *et al.*, 2003; Mainali & Lim, 2008).

Whitefly responses to olfactory cues over varying distances have provided inconsistent results. Previous studies have suggested that *T. vaporariorum* do not respond to long distance olfactory cues (Mound, 1962; van Lenteren & Noldus, 1990). However, structural analysis of *T. vaporariorum* antennae suggests whiteflies possess chemosensory sensilla enabling them to detect vapours (Mellor & Anderson, 1995b; a). Other researchers have found whiteflies respond to short-distance volatiles from host plants, conspecifics and plant extracts (Vaishampayan *et al.*, 1975; Li & Maschwitz, 1983; Mellor & Anderson, 1995b; a; Zhang *et al.*, 2004). In Chapter 3, vapours of rosemary oil were found to be toxic to adults in closed containers. It was theorized that toxic vapors would repel adult whiteflies and reduce adult settling on peppers. The results indicated that rosemary vapours, compared to olive oil vapours, did not repel whiteflies from settling on pepper plants. Experiments comparing whitefly entrapment on yellow sticky traps treated with reduced-risk sprays found none of the sprays significantly altered the number of whiteflies caught per trap. This contrasts previous work that found combining plant extracts with yellow sticky traps significantly increased whitefly entrapment (Gorski, 2004). Differences between the work herein and that of Gorski's (2004) could be due to the doses of extracts applied to the traps and the methods of application. Gorski (2004) applied 0.1 ml of extract using a paintbrush to a small part of the yellow sticky trap. In this current study, 0.5 ml of 50% extracts were sprayed directly on the traps. Previous work with cabbage loopers has found a direct dose relationship between insect attraction and deterrence (Akhtar *et al.*, 2007). Therefore, further evaluation of whitefly responses to different doses of plant extract vapours are recommended.

Information of whitefly gustation and mechanoreception responses is sparse. As phloem feeders, *T. vaporariorum* are known to discriminate between plant species and plant cultivars after short stylet probes into leaf surfaces. Unlike aphids, whiteflies are known to possess chemoreceptors and mechanoreceptors on the tip of their labium that may be used in host evaluation (Hunter *et al.*, 1996; Lei *et al.*, 1998; Storeck *et al.*, 2000; Powell *et al.*, 2006). For *T. vaporariorum,* the location of plant resistance factors depends upon the plant species (Lei *et al.*, 1999). In peppers, resistance factors were found on the leaf surface and in the mesophyll. In tomatoes, resistance factors were present in the phloem tissue. Other studies have explored the effects of leaf surface topography on whitefly plant resistance but again, responses tend to vary depending upon plant species (De Ponti *et al.*, 1990).

In early experiments conducted at UBC, a comparison of *T. vaporariorum* settling on sweet pepper cultivars suggested trends for higher densities on certain cultivars. It was theorized that whitefly preferences between commercial pepper cultivars would have a significant affect on settling and oviposition (Laska *et al.*, 1982; De Ponti *et al.*, 1990). However, the results of Chapter 4 found no significant difference in whitefly settling or oviposition on the specific pepper cultivars tested. A lack of differences between commercial cultivars Baselga, Fascinato and Orangery was attributed to a narrow range of plant material tested and broader comparisons evaluating more cultivars is recommended.

Consistent results between Chapter 2 and Chapter 5 were obtained from trap crop experiments with eggplant. In Chapter 2, eggplant reduced adult settling on peppers by 31% and oviposition by 27%. In chapter 5, eggplant reduced adult settling on peppers by 34% and oviposition by 28%. These results provide good evidence that eggplant trap crops can reduce whitefly adult and egg densities on peppers. However, strong significant differences were not obtained in both experiments. This is likely due to variability of the data points. Greenhouses have been suggested as worthy sites for trap crop management and commercial application of whitefly traps in poinsettia greenhouses has shown trap crops integrate well with biological control programs (Buitenhuis & Shipp, 2006; Murphy *et al.*, 2006). At the beginning of the study, I toured poinsettia greenhouses in Ontario to observe eggplants being used in combination with biological control agents to control *T. vaporariorum.* In some instances, eggplants were combined with yellow sticky traps but not all. For those growers currently using eggplant trap crops, it is recommended that yellow sticky traps be added to the trap crops to enhance adult trapping.

One of the limitations of trap crops is the amount of knowledge needed to implement a successful and predictable pest strategy (Shelton & Badenes-Perez, 2006). Insect characteristics that are deemed important for trap crop management include the insect stage targeted, the movement and dispersal behaviours of the insect, and its host-finding, acceptance and preference behaviours. Trap crops function by attracting or arresting insects. The arrestment strength of trap crops is considered more important than the attractiveness of the trap crops for insects with post-alighting host recognition behaviours (Potting *et al.*, 2005; Shelton & Badenes-Perez, 2006). For insects that use olfactory and visual cues during host selection, insect aggregation on trap crops was considered a combination of attraction and arrestment.

Evaluating the underlying mechanisms of trap crops, attraction versus arrestment, on *T. vaporariorum* behaviours proved beyond the scope of this project. Based on my experience with this system, I would hypothesize that both attraction and arrestment are involved and additional studies are needed to better understand the mechanisms of trap cropping for *T. vaporariorum*. In future studies, comparisons of whitefly departure rates between low-ranked and high-ranked hosts may help clarify attraction versus arrestment. For example, if whiteflies arrive to pepper and eggplant at equal frequencies, then comparing departure rates may indicate the arrestment strength of trap crops. Also, direct behavioural observations of whiteflies would be valuable.

Proper establishment and management of trap crops is of prime importance to the functioning of a given system (Hokkanen, 1991). Unhealthy trap crops can experience reduced trapping effectiveness and may become sources of pests rather than sinks. To avoid trap crops becoming a source of pests rather than a sink, pest populations on trap crops must monitored and controlled if required. This can be accomplished through the use of biological control agents, reduced-risk sprays, whole plant removal or pesticides. When controlling pest densities on trap crops, however, the effects of the control agents on pest behaviour must be considered ensuring that future trapping is not affected. Trap cropping is often used as part of an integrated pest management strategy. Several methods of increasing trap crop effectiveness have been described in the literature including combination with biological controls, resistant plant cultivars, crop rotation, and the addition of attractive semiochemicals (Hokkanen, 1991; Shelton & Badenes-Perez, 2006; Cook *et al.*, 2007). In this current project, visual cues from yellow sticky traps were found to increase trap crop efficacy. Additional study of combining trap crops with other control strategies is necessary to determine the degree to which trap crops can contribute to reducing whitefly populations on greenhouse-grown sweet peppers.

Whiteflies are pests not only for growers but also for researchers. In the early stages of this project, numerous experiments testing *T. vaporariorum* responses to trap crops and settling deterrents were attempted in both small-scale and commercial-scale greenhouses. Much was learned from these experiences. However, the results proved irreplicable due to wide range of variance exhibited by the whitefly specimens. A project intent on testing whitefly trap crops within greenhouses became a project focused on laboratory bioassays using cages as controlled experimental arenas. Despite the limitations of using laboratory data to make recommendations for larger greenhouses, the results provide quantified information on the individual and combined use of alternative whitefly control tactics. The complexity of insect responses to integrated cropping systems and to experimental conditions emphasizes the importance of understanding the ecological dynamics and the interacting influences affecting pest distribution. This is not an easy task. The variation in whitefly responses makes for challenging study. However, the opportunity of such a challenge may lead to new and novel control tactics.

In conclusion, manipulating whitefly behaviours using combinations of tactics indicated *T. vaporariorum* settling and oviposition can be directed away from peppers to traps. Behaviour manipulation of insect pests requires knowledge of cues that trigger predictable and innate actions based on the unique sensory abilities of a given pest. For *T. vaporariorum*, the greatest modifiers of *T. vaporariorum* settling and oviposition behaviours were YSTs > TCs > RRSs > PR. Results found trap crops combined with yellow cards reduced whitefly densities on crops by 53%. Although a 53% reduction in whiteflies is not sufficient control for commercial greenhouse growers, concentrating whiteflies at a predetermined site within greenhouses could improve whitefly management. Additional studies of whitefly vision and the combined use of yellow sticky traps + trap crops is recommended.

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