

HOST PLANT AND TEMPERATURE EFFECTS ON POPULATION DYNAMICS OF
THRIPS VECTORS OF *TOMATO SPOTTED WILT VIRUS*.

by

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(Under the direction of David G. Riley)

ABSTRACT

Ovipositional preference and reproduction of two thrips vectors of *Tomato spotted wilt virus* (TSWV) were investigated to determine plant host and TSWV effects on thrips population dynamics. The ovipositional preference between host plants (tomato and common chickweed (*Stellaria media* (L.) Vill.) with and without TSWV infection were also investigated with no choice and choice tests for whole plants in greenhouse cages and for leaf disks in growth chambers. Life tables of *F. occidentalis* and *F. fusca* were constructed from thrips feeding on leaf disks of different hosts (tomato and chickweed), plant age, temperature, photoperiod, and TSWV infection.

In a greenhouse study, *F. fusca* oviposited five times more eggs per plant than *F. occidentalis* on both tomato and chickweed regardless of TSWV infection. *F. fusca* also oviposited significantly more eggs in chickweed than tomato and non-TSWV infected plants than TSWV-infected plants. In ovipositional preference studies in growth chamber, both *F. fusca* and *F. occidentalis* oviposited more eggs per leaf disks at temperature 25°C (12L:12D) and at photoperiod 18L:6D (20°C) in all four combinations of plant species and TSWV-infection.

In partial life table parameter studies, both thrips species had no significant difference in net reproduction, generation time, and intrinsic growth rate, between two host plants with or without TSWV infection. Temperature and photoperiod significantly affected the three life table parameters. The intrinsic growth rates of *F. occidentalis* were negative at 20°C and under while the intrinsic growth rates under 15°C of *F. fusca* were projected to be negative. A temperature-dependence logistic population model for both species of thrips was calculated for both chickweed and tomato.

INDEX WORDS: Common chickweed, *Frankliniella fusca*, *Frankliniella occidentalis*, *Frankliniella tritici*, Generation time, Intrinsic growth rate, Life tables, *Lycopersicon esculentum*, Mortality, Net reproduction, Ovipositional preference, Population model, *Stellaria media*, Tobacco thrips, Tomato, TSWV, Western flower thrips

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DEDICATION

For people who help feed the world.

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CHAPTER 1

INTRODUCTION

Background and Purpose of the Study

Tomato spotted wilt virus (TSWV), family *Bunyaviridae*, genus *Tospovirus*, is a plant virus vectored by thrips (Thysanoptera: Thripidae). Currently, seven species of thrips in genera *Thrips* and *Frankliniella* are confirmed to be vectors of TSWV (Ullman et al. 2002). Two species, Western flower thrips, *Frankliniella occidentalis* (Pergande), and tobacco thrips, *F. fusca* (Hinds), have frequently been reported as major vectors in multiple crop systems in the Southeastern USA. The populations of *F. fusca* have been associated with TSWV incidences in agronomic crops, such as peanut (Chamberlin et al. 1992, Garcia et al. 2000) and tobacco (McPherson et al. 1999) while *F. occidentalis* populations were highly associated with TSWV incidences in vegetables, such as tomato (Aramburu 1997, Riley and Pappu 2000, Nault et al. 2003), and ornamental crops (Gofflot and Verhoyen 1990). A high percentage of *F. fusca* populations were also observed in pre-flowering tomato (Joost and Riley, in press) while *F. occidentalis* has been reported to be more prevalent in tomato flowers than other vector species (Riley and Pappu 2000, Salguero et al. 1991).

The infection of TSWV in young tomato plants early in the season can cause severe yield loss (Aramburu et al. 1998, Chaisuekul et al. 2003). The growing season of fresh market tomato in southern Georgia and northern Florida initiates in March-April in the spring and July–August in the fall. Coincidentally, the populations of *Frankliniella spp.* usually peak in April-May,

followed by a smaller secondary peak in September-October (Chellemi et al. 1994, Riley and Pappu 2000). *Frankliniella occidentalis* and *F. fusca* reportedly overwinter in weed hosts, such as wild radish, *Raphanus raphanistrum* L., and chickweed, *Stellaria media* (L.) Vill., in Southeastern US (Groves et al. 2002) while thrips overwinter as second instars or maintain their population in greenhouses in higher latitude (Kirk 1997). Brachypterous *F. fusca* are also important overwintering TSWV vectors (Chamberlin et al. 1992, Wells et al. 2002).

The specific role of *F. fusca* and *F. occidentalis* in vectoring TSWV in crop plants is still unclear relative to their individual ecology. *Frankliniella occidentalis* can be present in high number during blossom stage of tomato (Salguero et al. 1991). This led to the assumption that *F. occidentalis* plays major role in TSWV infection in tomato. However, the high density of *F. fusca* in early season of tobacco (McPherson et al. 1999), peanut (Chamberlin et al. 1992), and pre-flowering tomato (Joost and Riley 2004) suggests that it is also an important vector species. Additionally, early inoculation of TSWV to tomato plants has been reported to decrease yield more than later in the season (Chaisuekul et al., 2003). Earlier symptoms also correspond to lower tomato yield (Moriones et al. 1998). Thus, the thrips population and reproduction in pre-blossom crop plants as well as winter weed reservoirs may be important to help clarifying the epidemic of TSWV in economically important host plants. *Frankliniella fusca* was also implicated in transmission of TSWV from winter weeds to crop plants (Johnson et al. 1995, Groves et al. 2001, and Groves et al. 2002). The roles of these two thrips species in transmission of TSWV needs to be examined especially their reproductive successes relative to host plants and possibly TSWV infection.

TSWV was reported to have no significant impact on fecundity or longevity of infected *F. occidentalis* (Wijkamp et al. 1996). However, TSWV was observed in one experiment to

elevate mortality in infected thrips (G. Kennedy, seminar: “Population biology of thrips/virus interaction”, 7th International Symposium on Thysanoptera, July 2001). In Hawaii, higher number of thrips larvae was reported on TSWV-infected lettuce than on uninfected lettuce (Bautista et al. 1995) and host plant quality affected the preference and development of thrips (Bautista and Mau 1994). Besides TSWV, Impatiens Necrotic spot virus (INSV), a closely related plant virus to TSWV in genus *Tospovirus*, was found to have negative impacts on the reproduction and longevity of *F. occidentalis* (De Angelis et al. 1993). These studies demonstrate the variation in reported effects of TSWV-infected host plants on the reproduction and mortality of thrips. Additional information is obviously needed to help to understand the effects of epidemics of TSWV on the biology of its vectors.

Thrips vectors of TSWV are polyphagous, or in some case omnivorous herbivores, and they frequently encounter an array of possible host plants of differing suitability (Trichilo et al. 1988). Additionally, the ovipositional preference of a female unquestionably influences the fitness of her offspring (Van Nouhuys et al. 2003). The host plant preference is a trait of the herbivore to select suitable host plants for feeding and reproduction (Singer 2000). Host plant suitability is defined in this dissertation as the quality of specific plant material that influences the development and reproduction of herbivores. Host plant acceptability is the quality of a plant that influences the feeding of herbivores (Singer 2000). Reproductive success of insect herbivores is a key factor in the management of crop pests because it determines population levels and subsequent economic injury level (Kogan 1998). Besides host plant suitability, other biotic factors, such as competition both intra-specific and inter-specific, predation, parasitism, and abiotic factors, such as temperature, humidity, precipitation, and photoperiod, can influence the reproductive success of herbivores (Price 1997). The main thrips life stages, eggs, immatures,

and adults, affected by some of these factors are presented in Table 1.1. Immatures include first larva, second larva, prepupa, and pupa, and these life stages are named to distinguish feeding immatures with no wing structure (first larva and second larva) from non-feeding immatures with wing structures (prepupa and pupa), and these names do not imply that thrips has a complete metamorphosis. Not all factors affect all three major life stages of thrips. Host plant quality and temperature are two factors that could affect all three stages, and they were routinely reported to affect the reproduction of many insect herbivores (Price 1997).




Plant diseases could alter plant quality that affects plant's suitability and herbivore's preference and performance. Insect herbivores could be detrimentally affected by a disease either directly or indirectly, for example the virus reduces plant nutrients or induces plant defense mechanism which in turn offsets insect reproduction. For example, whiteflies, the vectors of plant Geminiviruses, were reported to decrease in reproduction due to infection of the viruses (Rubenstein and Czosneck 1997). The reproduction of thrips can be greatly affected by many factors relative to host plant quality, such as the availability of pollen versus just plant foliage, and other factors (Kirk 1997).

The management of TSWV is directly linked to the reproductive success of its thrips vectors. TSWV has spread across many parts of the world in part due to the reproductive effectiveness of its vectors. Thrips can reproduce sexually and parthenogenically, potentially doubling its population within a week (Lowry et al. 1992), but many details are still unknown. Life histories of thrips, especially population dynamics of *F. occidentalis*, were reported in several crop hosts, such as chrysanthemum, cotton, cucumber, peanut, pepper, and tomato (Boissot et al. 1998). Additionally, life table parameters were reported in a few selected crops, such as chrysanthemum (Katayama 1997, De Kogel et al. 1998), peanut (Lowry et al. 1992), and

cucumber (Guam et al. 1994, Soria and Mollema 1995, Van Rijn et al. 1995, De Kogel et al. 1997), and a weed, Jimson weed, (Wijkamp et al. 1996). Still, there is a lack of publications on the life history of *F. fusca*, the other major vector of TSWV in southeastern U.S.A. Also, life table data for *F. fusca* is needed in other crops besides peanut where the majority of general population dynamic data has been reported (McPherson et al. 1999). One area of study that has not been adequately addressed is direct comparison of different thrips vector species that coexist in a cropping system. A paired comparison of the reproduction of *F. fusca* and *F. occidentalis* in both a host crop and an important weed host is needed to begin understanding the relative importance of these two vector species in the epidemiology of TSWV in the Southeastern USA.

This research project focuses on two species of thrips vectors, *F. occidentalis* and *F. fusca*, which are the major TSWV-vectors for crops in Georgia, and two susceptible host plants, tomato and chickweed. Tomato was the first host plant on which TSWV was first detected, and there is no life history information of *F. fusca* on tomato. Also, reproduction on just foliage, prior to bloom formation has not been reported for either species. Chickweed was reported to be the most significant host of *F. fusca* in transmission of TSWV from winter weed to peanut (Groves et al. 2002), but chickweed as well as other winter weeds were not identified as a TSWV reservoir for *F. occidentalis*. Thus, thrips reproduction in both tomato and chickweed would elucidate the epidemiology of TSWV from winter weed to crop plants. Mechanical inoculation of TSWV is selected to be main method of transmission because of its consistency over thrips transmission (Chaisuekul et al. 2003). Pollen was not evaluated in these tests to narrow the focus of the research . However, pollen is known to have a major impact on flower thrips reproduction (Gerin et al. 1999), and would eventually have to be accounted for in a comprehensive population model for these species of thrips.

Table 1.1 Some major factors affecting thrips reproduction on plant foliage and the main growth stage(s) which they impact.

				
Factors	Reference	Egg	Immatures	Adult
Biotic Factors				
Host quality	Trichilo and Leigh 1988, Katayama et al. 1997	X	X (only first two feeding stage)	X
Host plant resistance	Annadana et al. 2002, Cardona et al. 2002		X (only first two feeding stage)	X
Competition -Intra-specific -Inter-specific	Crespi 1992, Kirk 1994 Kawai 1985		X X	X X
Predation	Sabelis and Van Rijn 1997	X	X	X
Parasitism	Greene and Parrella 1995,	X	X	X
Pathogen	Butt and Brownbridge 1997		X	X
Abiotic factors				
Temperature	Brosgaard 1993, Ishida et al. 2003	X	X	X
Photoperiod	Ishida et al. 2003	X	X	X
Relative Humidity	Lewis 1962, Shipp and Gillespie 1993	X	X	
Rainfall	Andrewartha and Birch 1954		X	X

Objectives and Expected Results

The goal of this research is to contribute basic information on the reproduction of thrips relative to epidemics of TSWV in vegetables, specifically in terms of ovipositional preference and partial life table data of two thrips vectors, *F. occidentalis* and *F. fusca* on pre-blossomed tomato and chickweed. This goal will be addressed in the following objectives:

- 1) To investigate the effect of two biotic factors, host plants (tomato vs. chickweed) and TSWV infection, on the reproduction of *F. occidentalis* and *F. fusca*.
 - 1.1) To determine ovipositional preference of *F. occidentalis* and *F. fusca*, between tomato and chickweed foliage (Chapter 3).
 - 1.2) To determine the reproductive parameters of *F. occidentalis* and *F. fusca* between tomato and chickweed foliage (Chapter 4).
- 2) To investigate the effect of two abiotic factors, temperature and photoperiod, on the reproduction of *F. occidentalis* and *F. fusca* feed on tomato and chickweed foliage.
 - 2.1) To determine ovipositional preference of *F. occidentalis* and *F. fusca*, on non-infected plant hosts, tomato and chickweed under selected temperature and photoperiod (Chapter 3).
 - 2.2) To determine the parameters of partial life tables of *F. occidentalis* and *F. fusca* on non-infected plant hosts, tomato and chickweed under selected temperature and photoperiod. (Chapter 4).
- 3) To investigate interactions between the above biotic (TSWV infection) and abiotic (temperature and photoperiod) factors and develop a simple population growth model based on these data.

- 3.1) To determine ovipositional preference of *F. occidentalis* and *F. fusca*, between TSWV-infected and non-infected plant hosts, tomato and chickweed under selected temperature and photoperiod (Chapter 3).
- 3.2) To determine the reproductive parameters of *F. occidentalis* and *F. fusca* between TSWV-infected and non-infected plant hosts, tomato and chickweed under selected temperature and photoperiod. (Chapter 4).
- 3.3) To determine the parameters of simple population growth model based on temperature for thrips on tomato and chickweed (Chapter 4).

The null hypothesis to be tested in these studies is that host plant, TSWV infection, and temperature have no effect on thrips ovipositional preference and reproduction. In the case of temperature effects, the hypothesis is that there is an optimum temperature for reproduction within the range tested.

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CHAPTER 2

LITERATURE REVIEW

Thrips vectors of TSWV

Tomato spotted wilt virus (TSWV) is the type member of the genus *Tospovirus* in the family *Bunyaviridae*, and while the genus *Tospovirus* contains plant viruses vectored by thrips, the other members in the family *Bunyaviridae* are mainly animal viruses (Brunt et al. 2000). Two genera of thrips (Thysanoptera: Thripidae), *Thrips* and *Frankliniella*, contain members that transmit TSWV. Currently, seven species of thrips, *Thrips tabaci* Lindeman, *T. setosus* Moulton, *Frankliniella occidentalis* (Pergande), *F. fusca* (Hinds), *F. schultzei* Trybom, *F. intonsa* Trybom, and *F. bispinosa* (Morgan), are confirmed to be vectors of TSWV (Ullman et al. 2002). These species were also found to vector some other tospoviruses besides TSWV (Ullman et al. 1997, 2002) (Table 2.1).

Thrips tabaci was the first vector of TSWV to be identified (Pittman 1927), and *F. occidentalis* and *F. fusca* were identified as vectors of TSWV about 20 years later (Sakimura 1963). During the 1980's, *F. occidentalis* was introduced to Europe from North America, and the re-emerging of TSWV in Europe was followed in late 1980's (Marchoux et al. 1991). Since then, the role of *T. tabaci* in transmitting TSWV has not been reported in North America or Europe, except parts of Eastern Europe (Chatzivassiliou et al. 2000, Ullman et al. 2002). *Frankliniella tenuicornis* (Uzel) and *Scirtothrips dorsalis* Hood had been previously reported to transmit

TSWV, but not experimentally proven (Ullman et al. 1997). *Frankliniella occidentalis* and *T. tabaci* transmit other plant viruses in addition to TSWV (Ullman et al. 1997).

Two major vectors of TSWV in the Southeastern USA are Western flower thrips, *Frankliniella occidentalis* (Pergande), and tobacco thrips, *F. fusca* (Hinds). The populations of *F. fusca* were reported to highly associate with TSWV incidences in agronomic crops, such as peanut (Chamberlin et al. 1992, Garcia et al. 2000) and tobacco (McPherson et al. 1999) while *F. occidentalis* populations were highly associated with TSWV incidences in vegetables, such as tomato (Aramburu 1997, Riley and Pappu 2000, Nault et al. 2003) pepper (Reitz et al. 2003), and ornamental crops (Gofflot and Verhoyen 1990). The high percentage of *F. fusca* populations were also observed in early stage of tomato while *F. occidentalis* were more prevalent in later stage and highly correlated with flowers (Riley and Pappu 2000, Joost and Riley, 2004).

The relative importance of *F. fusca* and *F. occidentalis* in transmitting TSWV in crop plants has not been determined. *Frankliniella occidentalis* can be present in high number during blossom stage of tomato (Salguero Narvas et al. 1991). This led to the assumption that *F. occidentalis* plays major role in TSWV infection in tomato. However, the high density of *F. fusca* in early season of tobacco (McPherson et al. 1999), peanut (Chamberlin et al. 1992), and tomato (Joost and Riley 2000), and early inoculation of TSWV to pre-blossomed tomato plants resulted in decreasing yield than later in the season to blossomed tomato plants (Chaisuekul et al., 2003). Thus, the thrips population and reproduction in pre-blossom crop plants as well as winter weed reservoirs may be important to help clarifying the epidemic of TSWV in economically important host plants. *Frankliniella fusca* was also implicated in transmission of TSWV from winter weeds to crop plants (Johnson et al. 1995, Groves et al. 2001, and Groves et al. 2002).

Table 2.1. Plant viruses transmitted by thrips in the genera *Frankliniella* and *Thrips* compiled from three reviews (Wijkamp et al. 1995, Ullman et al. 1997, Ullman et al. 2002).

Thrips species	Virus transmitted	Reference
<i>Frankliniella occidentalis</i>	<i>Tospovirus</i> : TSWV ¹ INSV ¹ GRSV ¹ , TCSV ¹ Pollen borne viruses: PNRSV ² , PDV ²	Gardner et al. 1935 De Angelis et al. 1993 Wijkamp et al. 1995 Greber et al. 1992
<i>F. fusca</i>	TSWV	Sakimura 1963
<i>F. bispinosa</i>	TSWV	Webb et al. 1992
<i>F. intonsa</i>	TSWV, TCSV, GRSV	Wijkamp et al. 1995
<i>F. schultzei</i>	TSWV, TCSV, GRSV	Samuel et al. 1930
<i>Thrips tabaci</i>	TSWV, PNRSV, TSV ² SoMV ³	Pittman 1927 Greber et al. 1991 Hardy and Teakle 1992
<i>T. setosus</i>	TSWV	Kobatake et al. 1984
<i>T. palmi</i>	WSMV ¹ GBNV ¹	Iwaki et al. 1984 Lakshmi et al. 1995

¹Bunyaviridae: (TSWV) *Tomato spotted wilt virus*, (TCSV) *Tomato chlorotic spot virus*, (GRSV) *Groundnut ringspot virus*, (INSV) *Impatiens necrotic spot virus*, (GBNV) *Groundnut bud necrosis virus*, (WSMV) *Watermelon silver mottle virus*

²Ilarviridae: (PNRSV) *Prunus necrotic ringspot virus*, (PDV) *Prune dwarf virus*, (TSV) *Tobacco streak virus*

³Sobemoviridae: (SoMV) *Sowbane mosaic virus*

Biology and Life Cycle of Thrips Vectors

Thrips (Thysanoptera) are closely related to other insects in hemipteroid assemblage, such as book lice (Psocoptera), lice (Phthiraptera), true bugs (Hemiptera), whiteflies and aphids (Sternorrhyncha), cicadas and treehoppers (Auchenorrhyncha) (Wheeler et al. 2001).

Several of these insects in hemipteroid assemblage have some forms of sucking mouthparts.

Thrips have asymmetric sucking mouthparts with mandible-piercing and maxillary stylets-sucking and are mainly detritivores and herbivores with some predators (Kirk 1997).

Herbivorous thrips were found to feed on plant materials as well as opportunistically feed on dead insects and mites eggs *F. occidentalis* (Trichilo and Leigh 1988), *F. schultzei*, and *T. tabaci* (onion thrips) (Wilson et al. 1996) were reported to feed on eggs of spider mite.

Although, insects in hemipteroid assemblage develop hemimetabolously, they are exopterygotes that most closely relate to endopterygotes which develop holometabolously (Wheeler et al. 2001). Thrips, though do not have complete metamorphosis, they do have two or three quiescent and non-feeding stages depending on suborder classification (Moriz 1997). Thrips vectors of TSWV in the genera *Frankliniella* and *Thrips* belong to suborder Terebrantia which have six life stages, egg, first larva, second larva, prepupa, pupa, and adult (Fig. 2.1), while thrips in suborder Tubulifera have the total of seven life stages with two pupal stage instead of one as in suborder Terebrantia (Moritz 1997).

The life cycle of most thrips vectors is approximately 12-16 days from egg to adult depending on temperature, photoperiod, host plants, and other factors (Boissot et al. 1998). Female adult thrips lay their eggs inside pre-slited plant tissue with their saw-like ovipositor, usually in floral tissue for *Frankliniella spp.* (Terry 1997). The larvae, wingless, hatch in about 2-3 days, survive in winter as diapaused first instars, and enter one more feeding stage as second larvae before entering the prepupal and pupal stages in the soil (Moritz 1997). The pupae emerge as winged adults, though some *F. fusca* are brachypterous, and migrate to plants by following visual and chemical cues (Terry 1997). Brachypterous adults of *F. fusca* were reported to migrate to adjacent peanut fields during late spring after overwintering in old peanut fields (Chamberlin

et al. 1992). *Frankliniella occidentalis* were reported to be able to overwinter and reproduce as adults (Buntin and Beshear 1995, Cho et al. 1995).

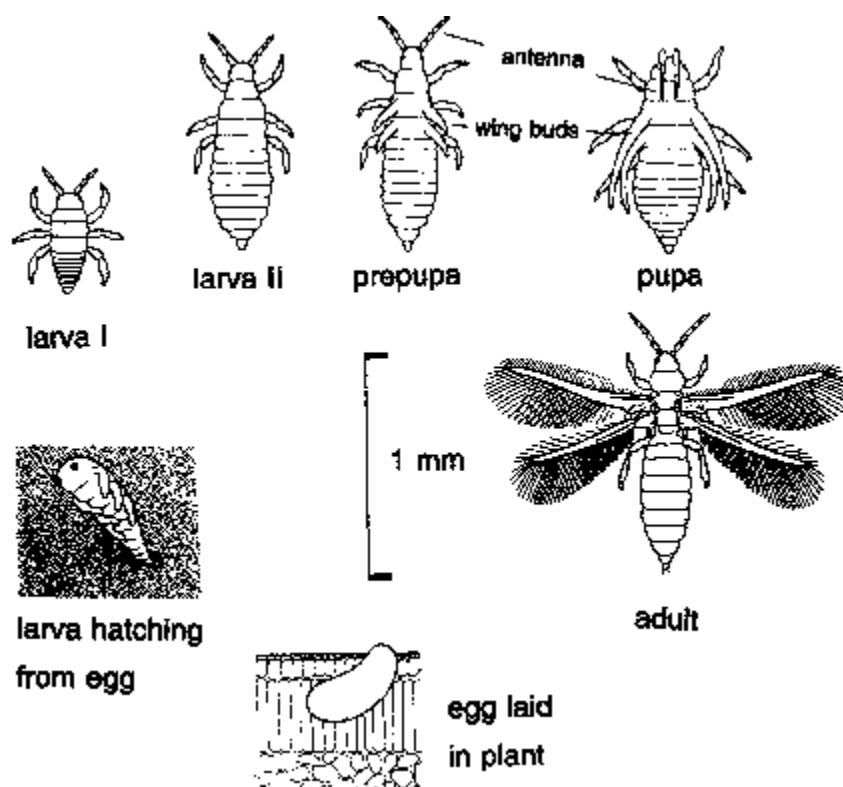


Fig. 2.1 Thrips life cycle (From Mound and Teulon 1995).

TSWV Transmission by Thrips.

Only immature thrips, usually first instars, are able to acquire TSWV. If they successfully acquire TSWV, thrips remains infectious through life, but they cannot pass the virus to offspring (Ullman et al. 1996). Adult thrips which did not acquire TSWV during their larval stages cannot transmit virus because of a midgut barrier (Ullman et al. 1992, de Assis et al. 2002). Female *F. occidentalis* have been shown to be less efficient in transmitting TSWV, even though female

thrips feed more than male thrips (Van de Wetering et al., 1998). *Frankliniella occidentalis* was reported as a more efficient vector for TSWV than *F. intonsa*, *F. schultzei* and *T. tabaci* on *Datura stramonium* (Wijkamp et al. 1995).

The close-association between TSWV and its thrips vectors is evident in the structure of the virus that contains lipid bilayer envelope and glycoproteins that facilitate the movement of the virus into thrips cells (Ullman et al. 2002). The replication of TSWV in thrips has been confirmed in several tissues, such as the foregut, midgut, salivary glands, and the ligament between midgut and salivary glands (Nagata et al. 1999, de Assis et al. 2002), but no evidence of TSWV in the haemolymph has been detected (Ullman et al. 2002). TSWV, instead of circulating through haemolymph to reach the salivary glands, moves along the ligament directly connecting the midgut and the salivary glands.

The successful acquisition and transmission of TSWV by thrips vectors is dependent on age. First and second instars of thrips are the only life stages that can acquire and transmit TSWV successfully with a higher rate in the first instar (van de Wetering et al. 1996). Non-feeding pre-pupa and pupa stages have no chance of acquiring TSWV while young adult thrips, less than 7 days after molting, may acquire TSWV, but fail to transmit the virus (de Assis et al. 2002). Immature thrips usually feed on the plant where they hatched due to their inability to actively fly. If that plant is infected with TSWV, first two instars can acquire the virus upon feeding and retain the virus through each molting. Thrips have piercing-sucking mouthparts that probe individual cells and rupture the cell content before sucking through their stylets. TSWV ingested by immature thrips is absorbed into midgut epithelial cells, then moves through the basal membrane to the midgut muscles (Nagata et al. 1999). Optimal transmission requires an

acquisition access period of 21 hours and in an inoculation access period of 43 hours (Wijkamp et al. 1996).

The viral encoded non-structural protein from medium RNA (NSm) of TSWV was found to facilitate plasmodesmatal cell to cell movement of the non-enveloped infectious ribonucleocapsid structures of TSWV in host plants (Kormelink et al. 1994, Storms et al. 1998). However, the function of the viral encoded non-structural protein from small RNA (NSs) has not yet been discovered (Ullman et al. 2002). Glycoproteins, G1 and G2, on envelope of TSWV bind specifically to 50-kDa proteins from midgut of thrips vectors while these glycoproteins do not bind with midgut proteins from non-vector thrips (Medeiros et al. 2000, Bandla et al. 1998).

The strain of TSWV, biotypes of thrips, vector species, and host plant cultigens widely differ across regions (van de Wetering et al. 1999). The outcome of these interactions can even be affected by difference of agricultural practices, such as the practice of mostly greenhouse production in Western Europe and Canada compared to more field crop production in the United States. TSWV transmission differences have been reported between different geographical populations of *F. occidentalis* (van de Wetering et al. 1999). The composition of alternative host plants, crops and weeds, will likely affect the thrips species composition in each region. Human activities facilitate the spread of TSWV in many ways. Increased insecticide resistance of thrips and the global trading of plant materials with possibility of thrips infestation allow thrips as well as tospoviruses to expand their hosts and geographic locations. Clearly, there are many things to consider when investigating thrips-TSWV interactions.

Host Plants in TSWV Epidemiology

Host plants must be susceptible to TSWV as well as reproductively suitable to thrips in order to serve as a reservoirs for the transmission of virus. Because only the first two instars of

thrips can successfully acquire and transmit virus, the host plants they feed on are usually the one where they emerge from eggs (Ullman et al. 2002). In this respect, the ovipositional preference of female thrips dictates the level of acquisition of TSWV. TSWV was first reported on tomato (*Lycopersicon esculentum* Mill) from Australia (Brittlebank 1919). Since then, TSWV has been reported to infect several host plants in at least 16 families, mainly in *Solanaceae* and *Leguminaceae* families (Brunt et al. 2000). Due to worldwide transportation, TSWV can spread with the shipment of infected plant products, infected plant stocks or carried with viruliferous thrips (Pitblado et al. 1990). TSWV-infected tomato and pepper stocks were imported from Georgia, and TSWV was spread to other host plants in Ontario, Canada as *F. occidentalis* dispersed (Pitblado et al. 1990). The number of thrips vectors especially *F. occidentalis* (Aramburu et al. 1997, Riley and Pappu 2000) and *F. fusca* (Chamberlin et al. 1992) were linked to the incidence of TSWV in field tomato and peanut, respectively.

Although some thrips vectors can feed on a wide selection of host plants, they appear to prefer particular host species or even host plant parts. *Thrips tabaci* (onion thrips) preferred to colonize leek (*Allium porrum* L.) comparing to inter-cropped strawberry clover (*Trifolium fragiferum* L.) (Den Belder et al. 2000). *Frankliniella occidentalis* (western flower thrips) and *F. schultzei* (common blossom thrips) are primarily pollen feeder and found associated with flowers (Terry 1997). Though *F. occidentalis* can survive and reproduce without pollen, they generally do not increase population size without pollen (Katayama 1997). *Thrips palmi* (melon thrips) have been reported to reproduce poorly on bell pepper (*Capsicum annuum* L.) comparing to winter melon (*Benincasa hispida* (Thunb.)), eggplant (*Solanum melongena* L.), and cucumber (*Cucumis sativus* L.) (Tsai et al. 1995). *Thrips palmi* was reported to avoid feeding on tomato (*Lycopersicon esculentum* Mill) due to tomatine, a glycoalkaloid in tomato (Hirano et al. 1994),

so this could be the reason that *T. palmi* does not transmit TSWV but transmits the other two *Tospoviruses*, GBNV and WSMV.

Most insect pests tend to preferably colonize crop plants over weeds because of the relatively high nutritional value and lower natural defenses in typical of crop plants. However, *F. occidentalis* and *F. tritici* Fitch (flower thrips: a non-vector for TSWV) were reported to primarily inhabit flowers of wild radish, *Raphanus raphanistrum* L., during winter in GA while *F. fusca* primarily inhabited on winter wheat, *Triticum aestivum* L., and winter rye, *Secale cereale* L., (Buntin and Beshear 1995). Wild radish has been positive for TSWV, though TSWV-infected wild radish were found in low percentage (<5%) under field condition (Groves et al. 2002). *Frankliniella fusca* also had differential preference on winter weed hosts, primarily preferring chickweed, *Stellaria media* Vill. Only Spiny sow thistle (*Sonchus asper*), common chickweed (*Stellaria media*), and common dandelion (*Taraxacum officinale*) were able to support substantial populations of *F. fusca* during winter (Groves et al. 2001).

TSWV Effects on Host plants

Symptom expression of plants infected with TSWV varies with plant species and cultivars (Kumar et al. 1993, Roca et al. 1997) and is affected by plant age (Moriones et al. 1998). Symptoms are generally similar to those caused by other plant viruses. Symptoms include stunting, leaf distortion, necrosis, wilting, mosaic, mottling and vein clearing (Moriones et al. 1998). Black necrotic spots and severe wilting are uniquely distinct to TSWV in which makes it easier to distinguish from other plant viruses. Irregular color patterns in flowers and fruits of tomato are generally found in TSWV-infected plants. Most flowers of infected tomato plants are pale yellow instead of normal bright yellow. Infected tomato fruits usually have mosaic or concentric rings after ripening.

Yield reduction was greater in TSWV-infected tomato plants with an early symptom expression than later symptoms (Moriones et al. 1998). A similar effect was reported independently for both thrips and mechanical transmission tomato plants that were inoculated at younger ages, 1-4 weeks after seeding (Chaisuekul et al. 2003). However, yield responses from tomato plants with thrips transmission at ages 5-8 weeks after seeding leveled off compared to a linear regressed response from tomato plants mechanically transmitted at similar ages (Chaisuekul et al. 2003). The quality of different ages of tomato plants probably contributes to explain the inconsistent level of TSWV-transmission of thrips over time.

The infection of TSWV in young tomato plants early in the season can cause severe yield loss (Aramburu et al. 1997, Chaisuekul et al. 2003). The growing season of fresh market tomato in southern Georgia and northern Florida is primarily started in March-April, and the populations of *F. occidentalis* and *F. fusca* usually reach primary peak in April-May and significantly smaller secondary peak in September-October (Chellemi et al. 1994, Riley and Pappu 2000).

Frankliniella occidentalis and *F. fusca* reportedly overwintered in weed hosts, such as wild radish, *Raphanus raphanistrum*, and chickweed, *Stellaria media*, in Southeastern USA (Groves et al. 2002). Thrips overwinter as second instars or maintain their population in greenhouses in higher latitudes (Kirk 1997).

TSWV-Thrips interactions

Thrips tabaci was first reported to be the major vector of TSWV in 1960s, but *F. occidentalis* became the major vector in 1980s (Ullman et al. 1997). *Thrips tabaci* was found to poorly transmit a recent strain of TSWV. The strain-specific interaction between TSWV and the thrips vector species that resulted in a shift to *F. occidentalis* may have been simply due to the greater reproduction capacity of *F. occidentalis*, especially on host plants with pollen. Even with

F. occidentalis, only a small percentage of immature thrips actually acquire TSWV (van de Wetering et al. 1996). All of these observations leads to an important question if TSWV directly or indirectly affects on thrips survival and reproduction. The status of *F. occidentalis* as a major vector of TSWV in the USA in the 1990's was challenged by the reports of *F. fusca* associated with TSWV incidence in peanut and tobacco (Eckel et al. 1996). Wijkamp et al. (1996) reported that there is no effect of TSWV on survivorship and fecundity of infected *F. occidentalis* while Bautista et al. (1995) reported higher number of immature thrips on TSWV-infected lettuce. All related reports are summarized in Table 2.2, but to date, no published report clearly shows a direct effect of TSWV on the population dynamics of thrips vectors to the extent that shifts in vector species could result.

TSWV was reported to have neither positive nor negative impact on fecundity or longevity of infected *F. occidentalis* (Wijkamp et al. 1996). However very recently, TSWV was found to elevate mortality in infected thrips (G. Kennedy, seminar: "Population biology of thrips/virus interaction", 7th International Symposium on Thysanoptera, July 2001). Higher number of thrips larvae was reported on TSWV-infected lettuce than on uninfected lettuce (Bautista et al. 1995). Besides TSWV, Impatiens Necrotic spot virus (INSV), a closely related plant virus to TSWV in genus *Tospovirus*, was found to have negative impacts on the reproduction and longevity of *F. occidentalis* (De Angelis et al. 1993).

Other plant viruses have been reported to have effects on the reproduction of insect herbivores either directly or indirectly. Whiteflies, the vectors of plant geminiviruses, were reported to decrease in reproduction due to infection of the viruses (Rubenstein and Czosneck, 1997). Some plant viruses were shown to have indirect effect to herbivores by altering nutrition of host plants. *Tobacco mosaic virus* was reported to increase the survival rate of Colorado

potato beetle by mean of increasing the level of nitrogen in infected plants (Hare and Dodds 1987). In some cases, herbivores are detrimentally affected when plant defenses are induced (Agrawal 1999). Since the plant defense to pathogens and herbivores commonly utilize jasmonic acid pathway (Preston et al. 1999), herbivores could be affected by induced defenses in plants infected with virus. Whiteflies, the vectors of plant geminiviruses, were reported to exhibit decreased reproduction due to infection with Tomato yellow leaf curl virus (TYLCV) (Rubenstein and Czosneck 1997). Plant virus could affect the nutrition of facultative phytophagous predators of herbivores. *Orius insidiosus*, a predator of thrips which is facultatively phytophagous, was negatively affected in terms of longevity and fecundity by feeding on soybeans infected with *Soybean mosaic virus* (Armer et al. 1999).

Table 2.2 The effects of tospoviruses, TSWV and INSV, infection on thrips vectors.

Thrips species	Virus transmitted	Effect of viral infection on vectors	
<i>Frankliniella occidentalis</i>	<i>Tospovirus:</i>		
	TSWV	Positive (immature)	Bautista et al.1995
	TSWV	Neutral	Wijkamp et al. 1995
	TSWV	Negative	G. Kennedy, per. comm.
	INSV	Negative	De Angelis et al. 1993
<i>Thrips tabaci</i>	TSWV	Neutral	Wijkamp et al. 1995

Thrips Life Table Studies

Reproductive success of insect herbivores is a key factor in the management of crop pests because it determines population levels and subsequent economic injury level. Reproduction depends on host plant suitability as well as other biotic factors such as competition both intra-

specific and inter-specific, predation, parasitism, and abiotic factors such as temperature, humidity, precipitation, and photoperiod (Price 1997). Host plant suitability is influenced by these abiotic factors and level of herbivoral damages.

Life histories of thrips, especially population dynamics of *F. occidentalis*, were reported in several crop hosts, such as chrysanthemum, cotton, cucumber, peanut, pepper, and tomato (Boissot et al. 1998). Life table parameters were also reported in a few selected crops, including chrysanthemum (Katayama 1997, De Kogel et al. 1998), peanut (Lowry et al. 1992), and cucumber (Guam et al. 1994, Soria and Mollema 1995, Van Rijn et al. 1995, De Kogel 1997^b), and a weed, Jimson weed, (Wijkamp et al. 1995). There are some data reported on the life history of *F. fusca*, the other major vector of TSWV in southeastern U.S., in peanut (Lowry et al. 1992).

T. tabaci was once reported to be a major vector of TSWV during 1950's –1960's, but this species was found to decline in efficiency of transmission of TSWV during 1980's and 1990's (Ullman et al. 1997). *Frankliniella occidentalis* now considered the most important vector of TSWV. The change in the main vector species of TSWV could arise from different reproductive strategy of *T. tabaci* and *F. occidentalis*. With only cucumber leaf disk as diet, *T. tabaci* had better net reproduction comparing to *F. occidentalis*, and females of *T. tabaci* oviposit most eggs early in their lives while females of *F. occidentalis* oviposit their eggs equally throughout their lives (Van Rijn et al. 1995).

The published life-table parameters of thrips listed in Table 2.3. demonstrate the intra- and interspecific variability in reproduction that can be observed. With *F. occidentalis* this variability can be accounted for in part by differences in temperature (Gaum et al. 1994), host plants and plant parts (Wijkamp et al. 1995), especially pollen (Hulshof et al. 2003). However,

there is some disparity in reproductive rates between researchers that have used the same host plant and temperature (Gaum et al. 1994 versus Van Rijn et al. 1995) that suggests that other factors could be involved. Strains of *F. occidentalis* are generally not accounted for in these tests, but most likely have an effect on reproductive potential based on observations between biotypes of other insects. The presence of pollen appears to have a very large positive influence on reproductive potential of *F. occidentalis* (Gerrin et al. 1999, Hulshof et al. 2003), but no comparable study has been done on *F. fusca*. I suspected that *F. fusca* would do better on only foliage than *F. occidentalis* because *F. fusca* are mainly foliage feeders and rarely found with flower sampling unlike *F. occidentalis*, *F. bispinosa*, *F. schultzei* or *F. intonsa* (Eckel et al. 1996, Riley and Pappu 2000), but that *F. occidentalis* would respond better than *F. fusca* with the availability of pollen in terms of net reproduction (Gerrin et al. 1999, Hulshof et al 2003).

Table 2.3. Life table parameters of thrips species that are vectors of TSWV on some host plants.

Thrips species	Host Plant	Plant part	Temperature (°C)	L:D	R ₀ (per female)	r (per day)	T (days)	References
<i>Frankliniella occidentalis</i>	<i>Cucumis sativus</i>	Leaf	20	16:8	5.00	0.064	25.2	Guam et al. (1994)
			25	16:8	6.04	0.140	12.8	
			30	16:8	8.48	0.212	10.1	
<i>F. occidentalis</i>	<i>Cucumis sativus</i>	Leaf	25	16:8	32	0.163	23	Hulshof et al. (2003)
<i>F. occidentalis</i>	<i>C. sativus</i>	Leaf, pine pollen	25	16:8	141	0.240	24	
<i>F. occidentalis</i>	<i>Cucumis sativus</i>	Leaf	25	16:8	22.1	0.166	20.1	Van Rijn et al. (1995)
<i>Thrips tabaci</i>	<i>C. sativus</i>	Leaf	25	16:8	27.5	0.176	20.4	
<i>F. occidentalis</i>	<i>Datura stramonium</i> (TSWV)	Leaf	25	16:8	15.11	0.140	19.44	Wijkamp et al. (1996)
	<i>D. stramonium</i> (non-TSWV)	Leaf	25	16:8	11.98	0.127	19.63	
	<i>Chrysanthemum morrifolium</i>	Leaf, petal, pollen	20	16:8	86.49	0.171	19.2	
<i>F. occidentalis</i>	<i>Arachis hypogea</i>	Leaf	25	14:10	2.25	0.02	15.55	Lowry et al. (1992)
			30	14:10	0	0	0	
			30	14:10	35.39	0.383	9.5	
<i>F. fusca</i>	<i>A. hypogea</i>	Leaf	25	14:10	4.60	0.07	21.61	
			30	14:10	16.01	0.16	17.51	
			30	14:10	16.01	0.16	17.51	

L:D=Photoperiod, L=light hours and D=dark hours. R₀=Net reproduction. r=Intrinsic rate of population growth. T=generation time.

Population Models for Thrips

Several factors, as presented in table 1.1, could affect the reproduction and population dynamics of thrips. These factors can be categorized into biotic and abiotic factors. Biotic factors, such as host plant quality, host plant resistance, and natural enemies including predation, parasitism, and pathogens, can be viewed as density-dependent factors since they directly regulate the population based on density of organism through mortality (Kirk 1997). Abiotic factors, such as temperature, photoperiod, precipitation, relative humidity, are normally referred as density-independent factors since they indirectly regulate the population usually through manipulation of the density-dependent factors (Kirk 1997). Density-dependence models were developed to explain and predict human population, such as Malthus's geometric (exponential) growth in 1798 and Verhulst's logistic growth in 1846, and later applied to other organisms, including insects (*Tribolium confusum*, *Drosophila spp.*) in early 20th century (Hutchinson 1978).

Exponential model can be presented as $dN/dt = rN$ which can be solved into

$$N_t = N_0 e^{rt}; \text{ where}$$

N_0 =initial population

N_t =current population

r =intrinsic rate of population growth

This model assumes unlimited resource allowing population to grow indefinitely, but natural populations normally face limitation in terms of food, space, or natural enemies. Thus, the logistic model includes limitation factor (carrying capacity: K) as

$dN/dt = rN(K-N)/K$ which can be solved as $N = K / (1 - e^{-rt})$ where

N = Number of individuals

r =intrinsic rate of population growth

t =time

K =carrying capacity

Several population models base on logistic growth with extra parameters included to account for feeding rate, time-lag, non-overlapping generation, cannibalism, or stochastic environmental factors, (Hutchinson 1978). As density-dependence models were improved based on logistic growth with additional environmental influences of carrying capacity, the first density-independence population model was proposed to explain the population of *Thrips imaginis* by Andrewartha and Birch (1954). Their model (regression model) was based on precipitation and temperature in term of degree-day without including the initial population in the model, and population density is the function of precipitation and temperature and their regression coefficients.

Regression model: $N = ax_1 + bx_2 + cx_3 + \dots$; where

N = number of individuals.

a =regression coefficient of factor x_1

The model accurately predicted the outbreak of *T. imaginis* (Andrewartha and Birch 1954). This was amid controversy related to the interpretation of the model relating to the debate of the roles of density-dependence and density independence in population growth (Kirk 1997). The density-independence model was proposed for the populations of thrips (Andrewartha and Birch 1954) with temperature and precipitation as the major causes of mortality. However, these two factors could have played an important role in the availability of the food source, in this case the rose blossom.

Food availability depends on environmental condition, especially temperature and precipitation. Air-temperature has the major effects on germination (Grundy and Mead 2000) and growth (Storkey and Cussan 2000) of chickweed. The base temperature for chickweed growth is at -1.7°C typical for a winter weed, and the germination probability of chickweed fitted logistic model on temperature (Grundt and Mead 2000). Germination of chickweed mainly depends on temperature, daily air temperature and daily soil comparing to water availability, daily soil moisture and daily precipitation (Grundy and Mead 2000). Tomato growth is also affected by temperature with plant being able to grow at temperatures as low as 10°C (Wada et al. 2001).

The logistic model, though it appears simplistic, fits to most population growth and its modification can be applied to many situations. The exponential model could as well fit the pioneering populations or the early part of logistic model (Hutchinson 1978). The regression model could apply to many populations but it requires extensive data in order to create and verify the model (Kirk 1997). In the case of thrips vectors of TSWV, both the logistic model and the regression model could be applied to their populations in winter weed and tomato crop, but the model in this study utilized the logistic model with temperature-dependent factors as presented in Chapter 4.

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CHAPTER 3

THE EFFECTS OF HOST PLANT, TEMPERATURE, AND PHOTOPERIOD ON
OVIPOSITIONAL PREFERENCE OF *FRANKLINIELLA OCCIDENTALIS* AND
F. FUSCA (THYSANOPTERA: THRIPIDAE)¹

¹Chaisuekul, C. and D.G. Riley. To be submitted to Economic Entomology.

Abstract

Host plant effects of tomato (*Lycopersicon esculentum* Mill) and chickweed (*Stellaria media* (L.) Vill.) foliage infected and uninfected with *Tomato spotted wilt virus* (TSWV) on the ovipositional preferences of two thrips, *Frankliniella occidentalis* (Pergande) and *F. fusca* (Hinds), were investigated for whole plants in greenhouse. In addition, the preference over leaf disks of the above host plants were investigated under the effects of temperature, 15-30°C at 12L:12D, and photoperiods, 6L:18D, 12L:12D, and 18L:6D at 20°C in growth chambers. *Frankliniella fusca* oviposited significantly more eggs per whole plant foliage over 7 d than *F. occidentalis* by an average ratio of 4:1 on both tomato (4.94 ± 0.47 to 1.87 ± 0.38) and chickweed (5.59 ± 0.48 to 1.12 ± 0.25) regardless of TSWV infection. While *F. fusca* preferred chickweed over tomato and *F. occidentalis* preferred tomato over chickweed, both *F. fusca* and *F. occidentalis* preferred to oviposit eggs on non-TSWV plants (5.61 ± 0.54 and 1.66 ± 0.34 , respectively) more than TSWV-infect plants (4.92 ± 0.41 and 1.33 ± 0.30 , respectively). Temperature and photoperiod did not change the host plant preferences of *Frankliniella fusca* and *F. occidentalis*. Both thrips species significantly oviposited more eggs per leaf disk across all temperatures, in chickweed (4.33 ± 0.79 and 3.96 ± 0.69 , respectively) than in tomato (3.15 ± 0.74 and 2.5 ± 0.64 , respectively). The optimum temperature for oviposition of *F. occidentalis* and *F. fusca* were at 24.5°C and 24.9°C, respectively. No significant difference was observed between no-choice test and choice test. Based on these results, *F. fusca* appears to have an important role as a vector of TSWV in early-season tomato since oviposition directly impacts viral acquisition.

Key words: Host choice, tobacco thrips, western flower thrips.

Introduction

Western flower thrips, *Frankliniella occidentalis* (Pergande), and tobacco thrips, *F. fusca* (Hinds) are two major vectors of tomato spotted wilt virus (TSWV), family Bunyaviridae, genus Tospovirus. TSWV incidence has been associated with *F. occidentalis* in tomato (Aramburu et al. 1997, Riley and Pappu 2000) whereas high density of *F. fusca* correlates TSWV incidence of tobacco (McPherson et al. 1999), peanut (Chamberlin et al. 1992). *Frankliniella occidentalis* usually feeds and reproduces in flowers and high density of *F. occidentalis* is normally observed during blossom stage of tomato (Salguero et al. 1991, Riley and Pappu 2000). However, relatively high densities of *F. fusca* were observed in pre-blossomed tomato (Joost and Riley 2004). As the infection of TSWV in young plants can cause severe yield loss (Moriones et al. 1998, Chaisuekul et al. 2003), it is important to understand the behavior of thrips vectors in pre-blossomed stage of the crop.

Thrips vectors of TSWV are polyphagous or in some case omnivorous herbivores, and they frequently encounter an array of possible host plants of differing suitability (Trichilo et al. 1988, Jansen et al. 2003). Thus, the ovipositional preference of a female unquestionably influences the fitness of her offspring (Van Nouhuys et al. 2003). The ovipositional choice of a female thrips vector determines the survivorship of her offspring as well as TSWV transmission (Ullman et al. 2002). TSWV can only be acquired by immature thrips vectors to be transmitted, usually in adult stage (Ullman et al. 2002), and the wingless immatures normally feed on the plants their eggs were oviposited (Terry 1997). Thus, the proportion of TSWV vectors and consequently the level of TSWV epidemics are partially determined by the ovipositional behavior of female thrips over non-TSWV hosts and TSWV hosts as well as weed reservoir hosts and crop hosts. The damage of TSWV infection to crop plants in Southeastern US greatly

occurs in early spring when the populations of thrips vectors are highest (Riley and Pappu 2000). Lower thrips populations generally occur in late-summer-early fall. *Frankliniella fusca* was implicated in transmission of TSWV from winter weeds to crop plants (Johnson et al. 1995, Groves et al. 2001, and Groves et al. 2002). *Frankliniella occidentalis* and *F. fusca* reportedly overwinter in weed hosts, such as wild radish, *Raphanus raphanistrum* L., and chickweed, *Stellaria media* (L.) Vill., in Southeastern US (Groves et al. 2002) while they overwinter as second instars or maintain their population in greenhouses in more northern latitudes (Kirk 1997). However, the factors affecting thrips vector migration from winter weeds to early spring crops have not been clearly identified. Therefore, we attempted to test one possible important factor, differential ovipositional preference between host plants.

We examined the oviposition behavior of *F. occidentalis* and *F. fusca* between vegetative chickweed, a winter weed reservoir of both *F. fusca* and TSWV, and pre-blossomed tomato, a representative early season crop host. We hypothesized that *F. occidentalis* and *F. fusca* would have no ovipositional preference to different host plant species or level of TSWV infection. The specific treatments evaluated were TSWV-infected tomato, non-infected tomato, TSWV-infected chickweed, and non-infected chickweed in greenhouse cages. Both choice and non-choice tests were used to evaluate ovipositional behavior. We also examined the oviposition behavior of both thrips species on leaf disk of the above host plants under the influence of temperatures (15°C, 17.5°C, 20°C, 22.5°C, 25°C, 27.5°C, and 30°C at 12L:12D) and photoperiods (6L:18D, 12L:12D, and 18L:6D at 20°C). We hypothesized that ovipositional preference and output of *F. occidentalis* and *F. fusca* over host plant species or TSWV infection were not affected by temperatures or photoperiod.

Materials and Methods

Thrips: Colonies of *F. occidentalis* and *F. fusca* were maintained on green bean in plastic cups (Groves et al. 2001). *Frankliniella occidentalis* were originally collected from wild radish flowers in November, 2000, Tifton, GA, and *F. fusca* were originally collected from peanut plants in May 2000, Tifton, GA. Natural populations of *F. occidentalis* collected from tomato blossoms in the summer and from wild radish in the winter and of *F. fusca* collected from tomato plant and peanut plant were occasionally added to the colonies to maintain genetic diversity.

Host Plants: Tomato (cv. Sunny, Agrow Seed Co., Kalamazoo, MI) was seeded in pot mixture in a room maintained at 30°C with 12L:12D (light: dark), and Chickweed (Thyme Garden Herb Company, Alsea, OR) was seeded in pot mixture at 15°C with 12L:12D. Plants were in 15cm diameter pots placed over 30x30 cm² at the center of the cage.

TSWV-Inoculation: Plants were mechanically inoculated 4 wk after seeding (with at least 2 true leaves) with either TSWV-infected or healthy tomato tissue macerated in inoculation buffer (0.1M Potassium phosphate dibasic (K₂HPO₄), 0.01M Sodium Sulfite (Na₂SO₃), 0.01M Mercaptoethanol) over leaf surface that was lightly dusted of carborundum powder. TSWV inoculum was collected from field TSWV-infected tomato from the Lang farm, Tifton, GA, in May 2002 and kept frozen at -70°C. Plants were kept in dark at 25°C for 24h before their leaves were rinsed with water. Plants were verified to have the infection with DAS-ELISA (Agdia TSWV-ELISA kit, Agdia Corp., Elkhart, IN).

Greenhouse experiment: There were total of 24 exclusion cages with 8 cages on each of three benches. Each was 50x50x120 cm³ in dimension made of wooden frames covered with white or ivory fine mesh chiffon (quality 3871, Shason Inc., Japan) with door closed with fasteners (Velcro®, Velcro USA Inc., Manchester, NH, USA) at one corner. Each cage was connected

with drip tubes for irrigation at the base of each of four plants per cage. The average day-time temperature in greenhouse was $30\pm0.3^{\circ}\text{C}$ during the experiment.

Each greenhouse exclusion cage contained four plants with the combinations of non-infected tomato, non-infected chickweed, TSWV-infected tomato, and TSWV-infected chickweed according to each of the following treatments (Table 3.1). One-choice treatments, 4 treatments per replicate, were consisted of four plants with the same plant species TSWV infection. The four-choice treatment, one treatment per replicate, consisted of four plants from each combination of plant species TSWV infection.

Twenty newly emerged adult thrips (5 males and 15 females) from each species were released in the center of each cage for 1 wk. Any immature and adult thrips on the whole plants were collected and identify after 1 week from releasing thrips into cage. Leaf samples were stained with lactophenol-acid fuchsin based on Nuessly et al. (1995) to aid in identifying ovipositional scar under stereo-microscope. Staining method used in this experiment, though did not directly identify thrips eggs, improved the visibility of the ovipositional scars which implied number of egg as female thrips laid one egg per one ovipositional site. Number of eggs were recorded by position of leaves. Number of leaves and size measurement of sampling leaves of tomato and chickweed were collected to calibrate leaf area. Each treatment was repeated twice for each thrips species, except for four-choice that was repeated four times.

Growth chamber experiment: All plants (1 wk after inoculation) and petri dishes were kept at specific temperature and photoperiod in growth chambers (Percival Scientific, Boone, IA). Plants and thrips in each treatment were kept under 12L:12D at the following temperatures, 15°C , 17.5°C , 20°C , 22.5°C , 25°C , 27.5°C , and 30°C , and two additional photoperiods were 6L:18D and 18L:6D at 20°C .

Five male and Fifteen females of newly emerged adult thrips (less than 1 d old) were placed in each 100x15mm plastic petri-dish (Fisherbrand®, Fisher Scientific, Pittsburgh, PA) with four 12mm leaf disks with combination of treatments similar to the green house experiment (Table 3.1) over moistened filter paper (90 mm Whatman® grade 1, Whatman International Ltd., Maidstone, England). After 7d, all adult thrips were removed, and each of four leaf disks was placed over moistened filter paper (15 mm Whatman® grade 1, Whatman International Ltd., Maidstone, England) in a well of 24 well cell culture cluster (Costar® 3524, Corning Incorporated, Corning, NY). Number of eggs in each leaf disk after 7 d were examined under microscope and each leaf disk was observed for any immature and adult over the next 20 d. The experiment was repeated twice for each combination of temperature and photoperiod, and each replicate had four no-choice tests and four choice tests.

Statistical analysis: Number of eggs and other life stages were compared between temperatures and photoperiods as well as plant species and TSWV infection using PROC GLM (SAS version 8, SAS Institute 1999). F-statistics for temperature were calculated using the mean square of interaction of replicate, host plant, virus and temperature as denominator. F-statistics for photoperiod were calculated using the mean square of interaction of replicate (included virus), host plant, and photoperiod and as denominator. F-statistics for choice test were calculated using the mean square of interaction of replicate, choice, and temperature as denominator.

Results

No immature thrips were observed from *F. fusca* over 7 d while there were substantial immatures of *F. occidentalis* (0.57 ± 0.19) over 7 d (Fig. 3.2). However, *F. fusca* oviposited significantly more eggs per plant than *F. occidentalis* ($F=37.42$, $df=1,84$, $P<0.01$) by an approximate ratio of 4:1 on both tomato (4.88 ± 2.40 to 1.90 ± 1.87) and chickweed (5.58 ± 2.33 to

1.12±1.21) regardless of TSWV infection (Fig.3.3A). While *F. fusca* oviposited more eggs in chickweed than in tomato and *F. occidentalis* oviposited more eggs in tomato than chickweed, both *F. fusca* and *F. occidentalis* preferred to oviposit eggs on non-TSWV plants (5.61±0.54 and 1.66±0.34, respectively) than TSWV-infected plants (4.92±0.41 and 1.33±0.30, respectively) (Fig. 3.3B).

Although there was no significant effect of interaction between plant species and TSWV infection in *F. occidentalis*, there was a significant interaction between plant species and TSWV infection in *F. fusca* ($F=5.03$, $df= 1,84$, $P=0.03$). This interaction resulted in the highest number of eggs in non-TSWV tomato (5.81±0.59) compared to the lowest number of eggs in TSWV-infected tomato (4.07±0.31) (Fig 3.4A). Although, there were no overall significant difference of the oviposited eggs between no choice, two-choice, and four-choice tests ($F=0.93$, $df= 2, 84$, $P=0.34$), the number of eggs of *F. occidentalis* in TSWV-infected tomato are considerably higher in four choice test (2.12±0.78) than in one choice (0.50±0.02) (Table 3.2). There was no significant effect of bench, cage or plant position within a cage to the number of eggs in each plant in *F. fusca* as well as no effect of cage or plant position to the number of eggs in each plant in *F. occidentalis*. However, there were significant effect of bench in the *F. occidentalis* test ($F=4.21$, $df= 2,42$, $P=0.03$) with one bench (one choice test) had more number of eggs and immatures than the other remaining two benches.

Since tomato and chickweed plants used in the experiment, though has the similar age, had significantly different size of leaves (6.4 cm² per tomato leaflet to 1.2 cm² per chickweed leaf) and number of leaves (17.0±3.8 tomato leaflets to 8.9±2.1 chickweed leaves), the number of eggs per leaf area were calculated by thrips species, plant species, and TSWV-infection as

presented in Fig 3.4B. Both *F. fusca* and *F. occidentalis* oviposited more eggs per leaf cm² in chickweed (0.52 ± 0.15 and 0.10 ± 0.08) than in tomato (0.05 ± 0.05 and 0.02 ± 0.04).

Temperature significantly affected the number of eggs in each leaf disk for *F. occidentalis* ($F=4.81$, $df=6,6$, $P=0.04$) and *F. fusca* ($F=3.30$, $df=6,6$, $P=0.03$). *Frankliniella fusca* and *F. occidentalis* oviposited more eggs per leaf disk across all temperatures, in chickweed (4.33 ± 0.79 and 3.96 ± 0.69 , respectively) than in tomato (3.15 ± 0.74 and 2.88 ± 0.64 , respectively). The optimum temperatures for oviposition of *F. occidentalis* and *F. fusca* calculated from regression equation in Fig 3.5 A were at 24.5°C and 24.9°C, respectively. The number of eggs of *F. fusca* at 25°C was extremely higher than the other temperatures used in this experiment and was higher than the expected value calculated from regression curve (Fig 3.5 A) while *F. occidentalis* oviposited eggs significantly lower than *F. fusca* at 25°C, but not at the other temperatures. Both thrips species slightly preferred to oviposit on non-TSWV infected tomato leaf disks compared to the other three types of leaf disks across all temperatures (Fig 3.6 A and B).

Numbers of eggs were significantly affected by photoperiod in both *F. occidentalis* ($F=12.36$, $df=2,6$, $P=0.006$) and *F. fusca* ($F=13.95$, $df=2,6$, $P=0.007$), and they appeared to increase exponentially to photoperiod (Fig 3.5 B). Both thrips species did not significantly preferred any of the four types of leaf disks more or less than one another across all photoperiods (Fig 3.7 A and B). There was no significant difference between no-choice and four-choice tests in both *F. occidentalis* ($F=2.11$, $df=1,8$, $P=0.20$) and *F. fusca* ($F=1.13$, $df=1,8$, $P=0.32$) (Fig 3.8 A and B).

Discussion

Although *F. occidentalis* did not oviposit eggs as much as *F. fusca*, some immatures of *F. occidentalis* emerged in 7 d compared to none from *F. fusca* (Fig. 3.2), so *F. occidentalis* could acquire and transmit the virus faster than *F. fusca*. Both thrips species ovipositionally preferred non-TSWV tomato and chickweed over TSWV-infected tomato and chickweed, respectively (Fig 3.3B and Fig 3.4A). However, *F. fusca* and *F. occidentalis* have different ovipositional preference between chickweed and tomato. *Frankliniella fusca* appeared to prefer chickweed over tomato while *F. occidentalis* appeared to prefer tomato over chickweed (Fig 3.3A and Fig. 3.4A). When leaf area of the plants used in the experiment was taken in consideration, both thrips species oviposited more eggs per leaf area in chickweed than in tomato regardless of TSWV-infection (Fig 3.4B). Therefore, we reject the null hypothesis that *F. fusca* and *F. occidentalis* have no different ovipositional preference to different host plant species or TSWV infection.

Frankliniella fusca reportedly overwinter in chickweed (Groves et al. 2001) as well as vectoring TSWV to young tomato plants in early spring (Joost and Riley 2004). The result from this study supported the role of *F. fusca* in vectoring TSWV from winter reservoir weed to crops. The females of *F. fusca* had higher ovipositional preference for chickweed over tomato, especially TSWV-infected tomato. This study suggested the possible negative effect of TSWV infection to thrips vectors that influences the ovipositional preference of the two thrips vectors. Although TSWV-infected host plants appeared to have lower number of both thrips species, there were still considerable amount of eggs on these plants, so the adverse effects of TSWV infected plants may not be large. The TSWV-infection might not really have an effect on the

quality of the plants but maybe through direct pathological effects, such as reduced fecundity, on the thrips themselves due to TSWV replication inside the thrips body.

The temperature did not affect on the oviposition preferences of both thrips species since the preference on each type of leaf disk was consistent across all temperatures (Fig 3.6 A and B). Due to limited number of replication by species (2) and only 3 photoperiods used in this experiment, photoperiod significantly affected the number of eggs in both species when the treatments with or without TSWV infection were included as replicates. More replication or more photoperiod treatments would show significant effects of photoperiod as the seven levels of temperature treatments allowed the distinct statistical test between each level without including TSWV- treatment as replication.

With foliage as the only food source, *F. fusca* was more fecund than *F. occidentalis* over 7 d period in both chickweed and tomato with and without TSWV infection across all temperatures and photoperiods used in this experiment. However, the presence of pollen in the diet would favor *F. occidentalis* to be more fecund (Gerrin et al. 1999) while the pollen effect on *F. fusca* is not known. The migration of these two thrips vectors from chickweed as winter reservoir host to early spring tomato in the southeastern USA is probably not caused by the oviposition preference of tomato over chickweed or the changing of oviposition preference under changing temperature or photoperiod, but rather from other factors, such as seasonal host plant availability or population density exceed carrying capacity of chickweed.

The staining of leaves with lactophenol-acid fuchsin were required to aid in observing eggs over vast area of leaves since most eggs were embedded inside the leaf tissue. However, this method could not allow the follow up the survivorship of the eggs. The leaf disk experiment provide the method to observe the survivorship of eggs, especially of *F. fusca*, that did not hatch

within the 7 d, but the effects of leaf disk on the ovipositional preference may be differ from the whole plant as well as the plants in field environment. The damages caused by cutting of leaves to create leaf disks may induce the releasing of volatile compounds that could deter or attract the female thrips (Agrawal 1999). Some differences between the no-choice and choice tests in the greenhouse experiment (Table 3.2) were not found in the leaf disk experiments (Fig. 3.8) The presence of natural enemies or near by pollen source may influence the behavior of the female thrips to select a particular plant in the field condition (Van Nouhuys et al. 2003). Besides the ovipositional preference, the follow up studies in the reproduction of the two thrips species on these plants are required to assess the full effects of TSWV infection and host plants on the population growth of the thrips vectors.

Table 3.1. Number of plants in a greenhouse cage or number of leaf disks in a petri-dish in each choice treatment in for each thrips species.

Treatment/Plant	Rep/species	Non-infected tomato	TSWV- infected tomato	Non-infected chickweed	TSWV- infected chickweed
No-Choice					
1	2	4	-	-	-
2	2	-	4	-	-
3	2	-	-	4	-
4	2	-	-	-	4
Four-Choice					
	4	1	1	1	1

Table 3.2. Number (mean±SE) of eggs and immatures per plant over 7 d by 5 males and 15 females of *Frankliniella fusca* and *F. occidentalis* by choice treatments.

Treatments	<i>F. fusca</i>			<i>F. occidentalis</i>		
	n	egg	immature	n	egg	immature
No-Choice	32	5.64±1.00	0	32	1.44±0.23	0.75±0.25
1 TSWV tomato	8	4.14±0.52a*	0	8	0.50±0.20a	0.50±0.20a
2 Non-TSWV tomato	8	5.86±1.12ab	0	8	2.38±0.53c	1.25±0.36b
3 TSWV chickweed	8	6.14±0.90b	0	8	1.12±0.35b	0.38±0.18a
4 Non-TSWV chickweed	8	6.43±1.34b	0	8	1.00±0.27ab	0.75±0.41ab
Four-Choice	16	5.08±0.90	0	16	1.54±0.91	0.34±0.20
1 TSWV tomato	4	4.18±0.70a	0	4	2.12±0.78a	0.12±0.18a
2 Non-TSWV tomato	4	4.89±0.81a	0	4	2.25±0.80a	0.88±0.50b
3 TSWV chickweed	4	6.40±0.63b	0	4	0.88±0.36b	0.25±0.20a
4 Non-TSWV chickweed	4	4.86±0.35a	0	4	0.88±0.19b	0.12±0.10a

*Least square difference, same letter means no significant difference.



Fig. 3.1. Comparative size of chickweed leaves (4 wk) and a tomato leaflet (4 wk).

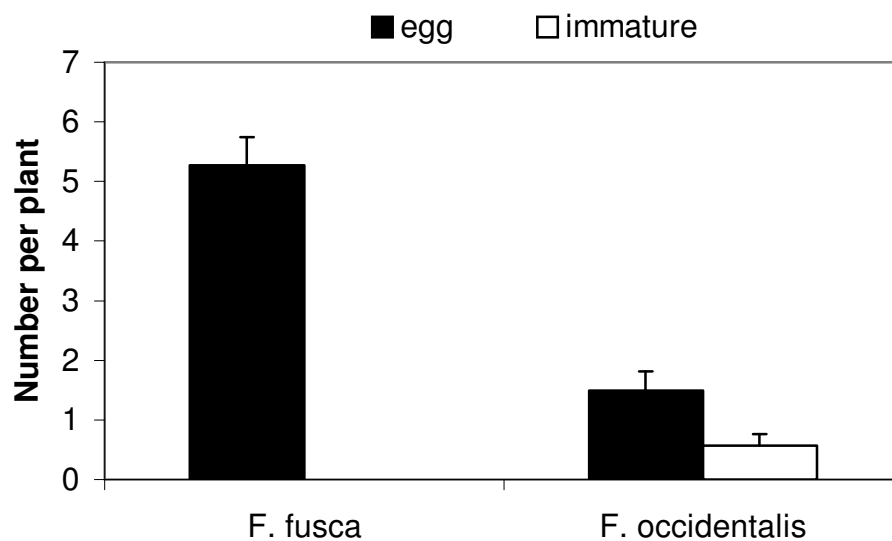
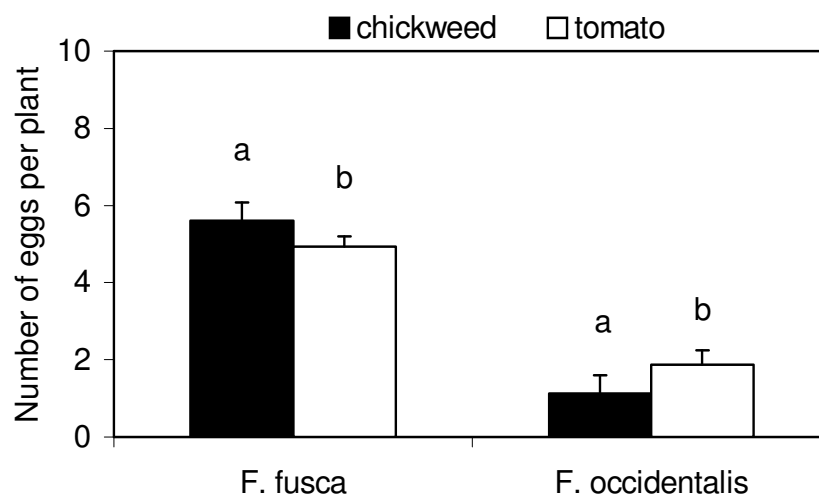


Fig. 3.2. Number of eggs and immatures per plant oviposited by *Frankliniella fusca* and *F. occidentalis* (15 females with 5 males per species) over 7 d combined over TSWV-infected tomato, non-TSWV tomato, TSWV-infected, and non-TSWV chickweed.

A) Host plant



B) TSWV infection

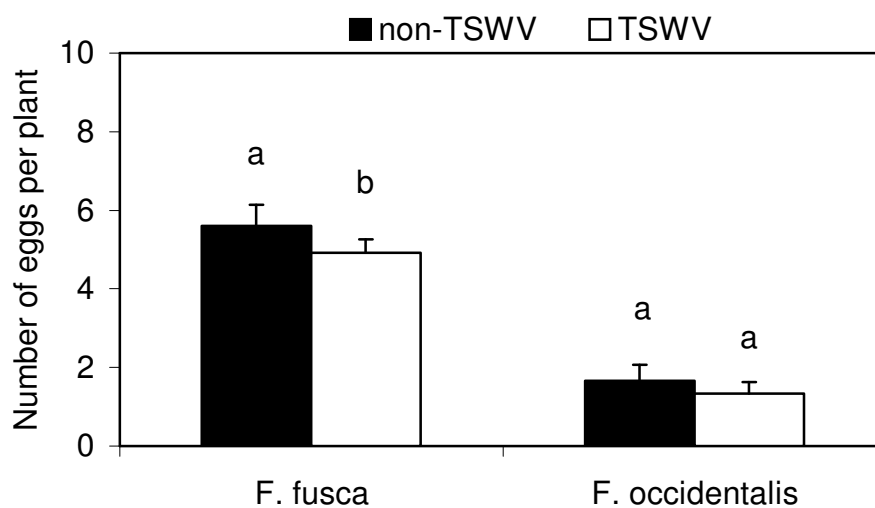
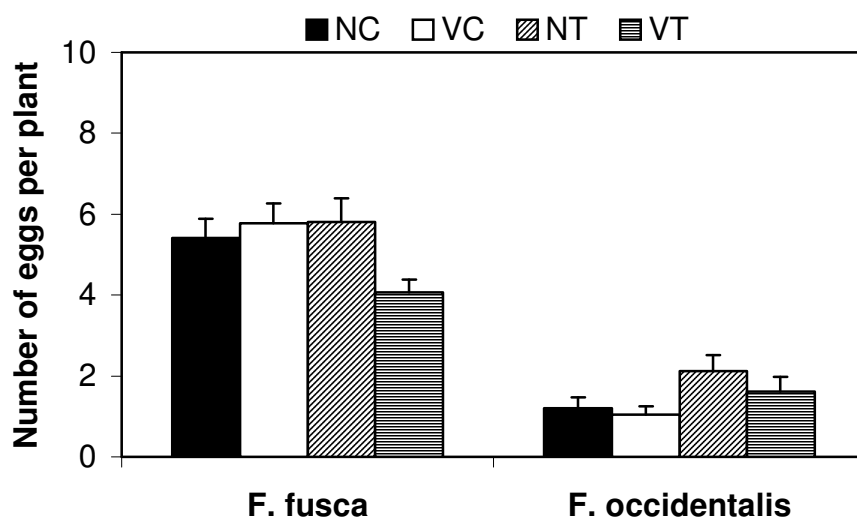


Fig. 3.3. Number of eggs per plant laid by 15 females with 5 males thrips by thrips species, *Frankliniella occidentalis* and *F. fusca*, over 7 d by **A)** host plant species and **B)** TSWV infection.

A) per Plant



B) per Leaf Area

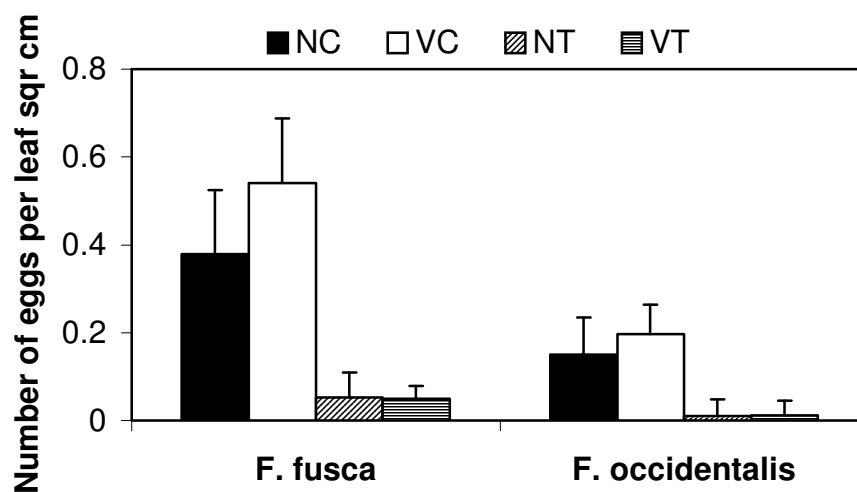
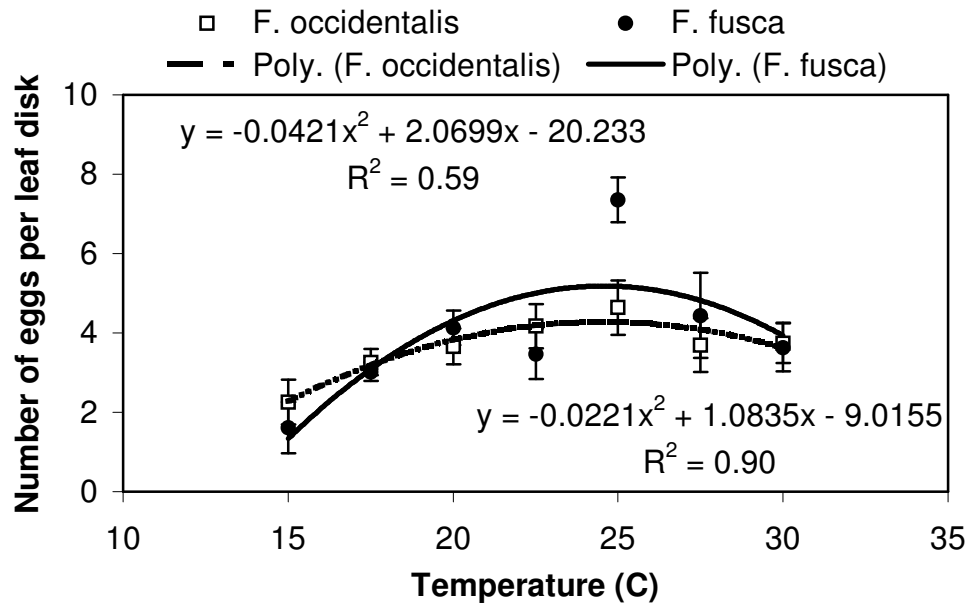


Fig. 3.4. Number of eggs laid by 15 females with 5 males thrips by thrips species, *Frankliniella occidentalis* and *F. fusca*, over 7 d per **A)** plant and **B)** leaf area (cm^2) by four plant types, 1. NC: Non-TSWV Chickweed, 2. VC: TSWV-infected Chickweed, 3. NT: Non-TSWV Tomato, and 4. VT: TSWV-infected Tomato.

A) Temperature



B) Photoperiod

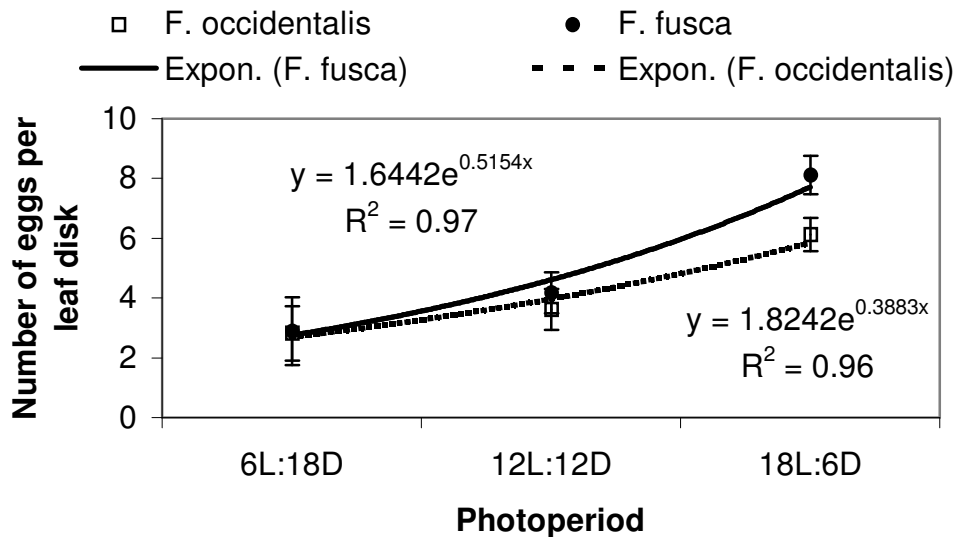


Fig. 3.5. Number of eggs oviposited by *Frankliniella occidentalis* and *F. fusca* per 12 mm leaf disk per 15 females over 7d from the combination of tomato and chickweed leaf disk across **A)** temperature 15°C, 17.5°C, 20°C, 22.5°C, 25°C, 27.5°C, and 30°C at 12L:12D, and **B)** photoperiod, 6L:18D, 12L:12D, and 18L:6D at 20°C.

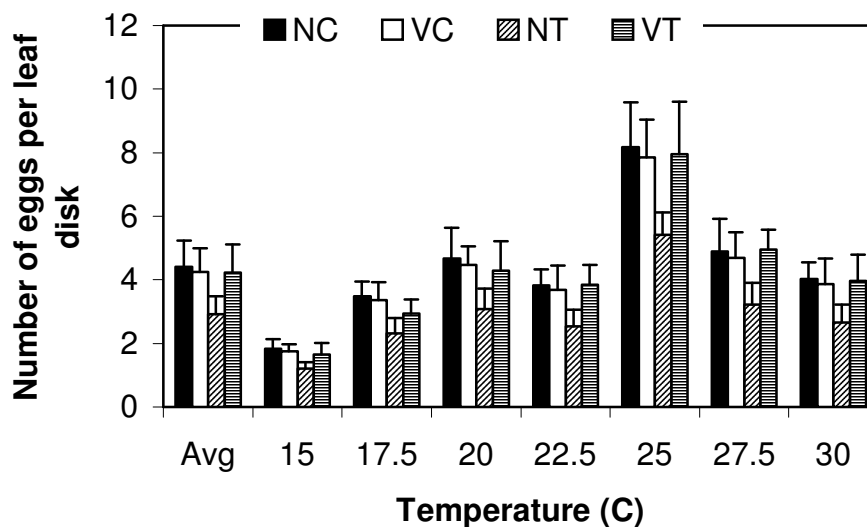
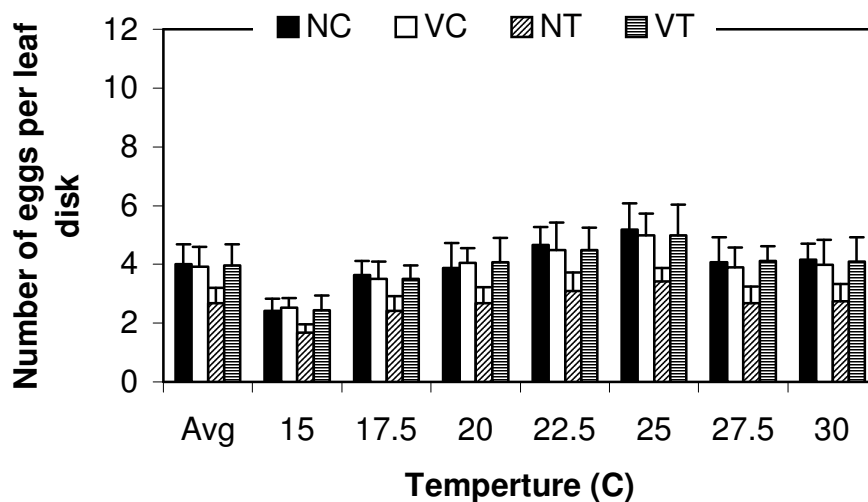
A) *F. fusca*B) *F. occidentalis*

Fig. 3.6. Number of eggs oviposited by A) *Frankliniella fusca* and B) *F. occidentalis* per 15 females over 7d on a 12 mm leaf disk by four types of leaf disks, 1. NC: Non-TSWV Chickweed, 2. VC: TSWV-infected Chickweed, 3. NT: Non-TSWV Tomato, and 4. VT: TSWV-infected Tomato across temperature 15°C, 17.5°C, 20°C, 22.5°C, 25°C, 27.5°C, and 30°C at 12L:12D.

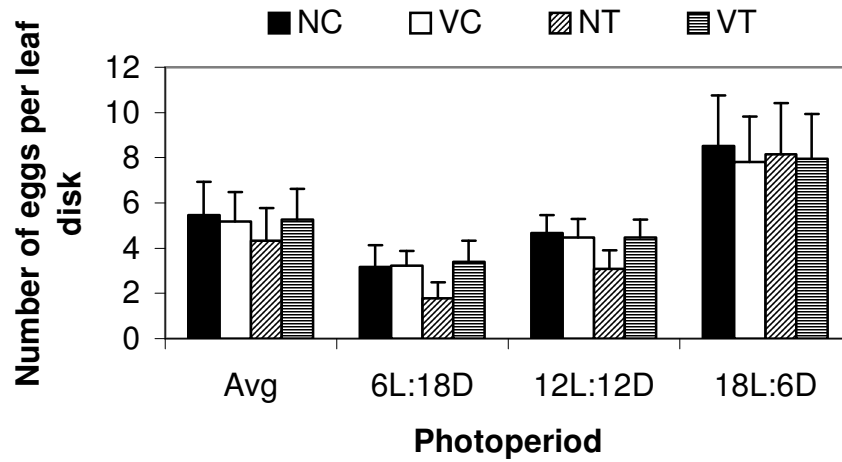
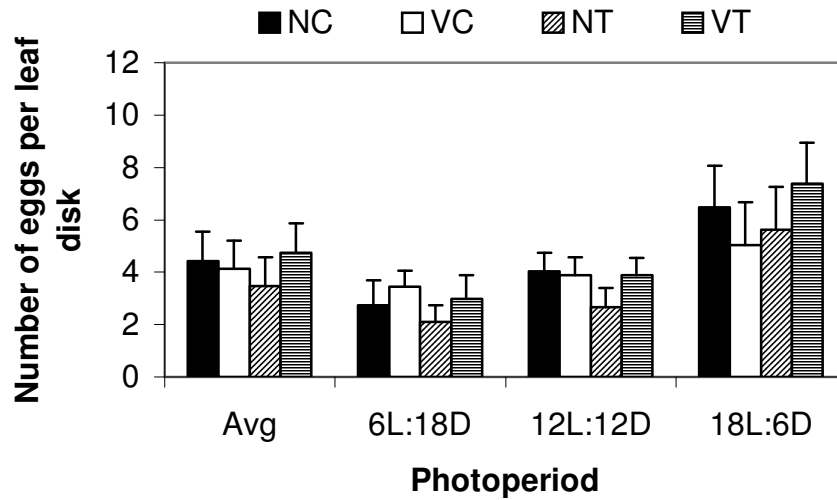
A) *F. fusca*B) *F. occidentalis*

Fig. 3.7 Number of eggs per leaf disk of **A)** *Frankliniella fusca* and **B)** *F. occidentalis* by 15 female thrips with 5 male thrips over 7 d on a 12 mm leaf disk by four types of leaf disks, 1. **NC**: Non-TSWV Chickweed, 2. **VC**: TSWV-infected Chickweed, 3. **NT**: Non-TSWV Tomato, and 4. **VT**: TSWV-infected across photoperiods, 6L:18D, 12L:12D, and 18L:6D at 20°C.

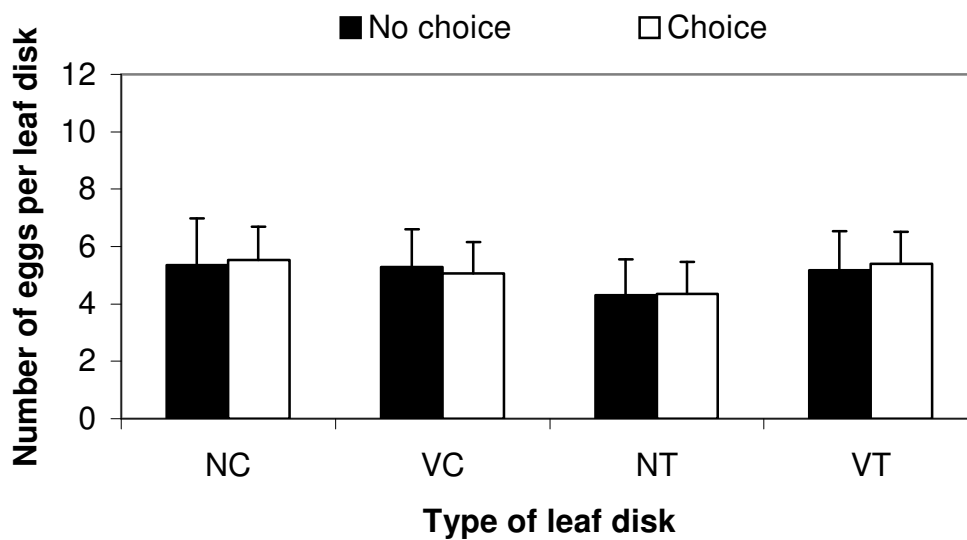
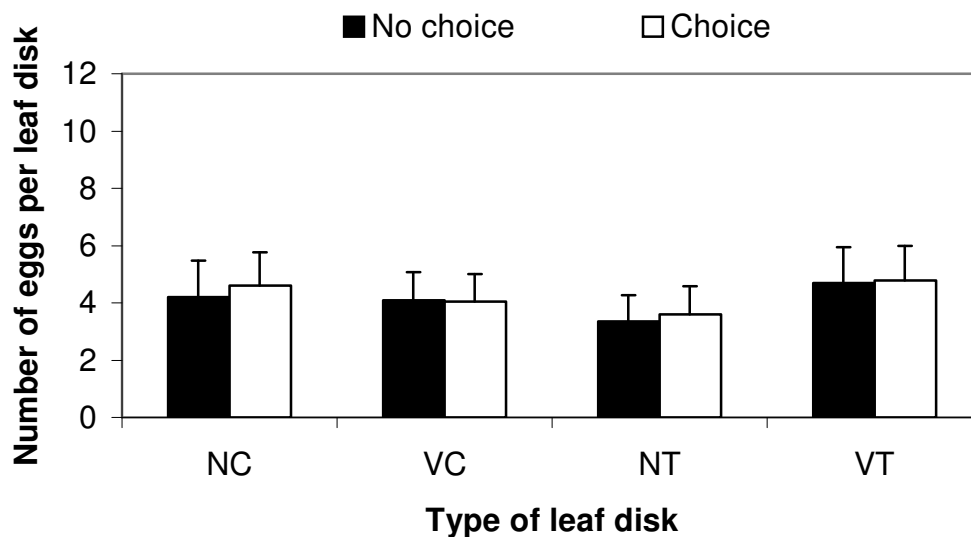
A) *F. fusca*B) *F. occidentalis*

Fig. 3.8 Number of eggs per leaf disk of **A)** *Frankliniella fusca* and **B)** *F. occidentalis* by 15 female thrips with 5 male thrips over 7 d on a 12 mm leaf disk between no-choice and choice tests on four types of leaf disks, 1. **NC**: Non-TSWV Chickweed, 2. **VC**: TSWV-infected Chickweed, 3. **NT**: Non-TSWV Tomato, and 4. **VT**: TSWV-infected Tomato.

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CHAPTER 4

HOST PLANT, TEMPERATURE, AND PHOTOPERIOD EFFECTS ON REPRODUCTION
OF *FRANKLINIELLA OCCIDENTALIS* AND *F. FUSCA* (THYSANOPTERA: THRIPIDAE)¹

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Abstract

Reproduction of two species of *Tomato spotted wilt virus* (TSWV) vectors were investigated in relation to species and infection of host plants as well as temperatures and photoperiods. The reproductive parameters and life-stage specific mortality of western flower thrips, *Frankliniella occidentalis* (Pergande), and tobacco thrips, *F. fusca* (Hinds), were compared between leaf disks of TSWV-infected non-infected tomato, *Lycopersicon esculentum* Mill and chickweed, *Stellaria media* (L.) Vill. across a range of temperatures 15-30°C, and photoperiod 6L:18D-18L:6D. Host plant significantly affected the net reproduction of *F. fusca* but not in *F. occidentalis*. *Frankliniella occidentalis* reproduced poorly on both chickweed and tomato with only leaves as a food source, ($R_0=1.01$, $r=0.0005$, $T=12.2$ and $R_0=0.92$, $r=-0.006$, $T=12.7$, respectively) while *F. fusca* reproduced significantly better on chickweed ($R_0=2.51$, $r=0.0652$, $T=14.1$) than on tomato ($R_0=2.31$, $r=0.0597$, $T=14.0$). Temperature had significant effects on the rate of population growth of both *F. occidentalis* and *F. fusca*. The optimum temperature for the reproduction of *F. occidentalis* (26.6°C) was lower than that of *F. fusca* (27.6°C) while the minimum temperature for reproduction of *F. occidentalis* (12.6°C) was higher than that of *F. fusca* (11.5°C). The lack of pollen in early spring crops and the poor reproduction of *F. occidentalis* in foliage suggest that *F. fusca* might be a more important vector of TSWV than *F. occidentalis*. The temperature-based population model allow limited prediction of thrips population in early spring condition, and other factors, such as precipitation and natural enemies, could allow more precise prediction.

Key words: Generation time, Intrinsic rate, Net reproduction.

Introduction

Tomato spotted wilt virus (TSWV), family Bunyaviridae, genus *Tospovirus* is a plant virus vectored by thrips (Thysanoptera: Thripidae). Two species, western flower thrips, *Frankliniella occidentalis* (Pergande), and tobacco thrips, *F. fusca* (Hinds), are reported as major vectors in the Southeastern USA (Chamberlin et al. 1992, McPherson et al. 1999, Riley and Pappu 2000, Nault et al. 2003). The reproductive capability of the thrips vectors influences the available number of vectors and the disease pressure. There were several publications on the reproduction parameters, net reproduction (R_0), generation time (T), and intrinsic growth rate (r), of *F. occidentalis* on varieties of conditions (Gaum et al. 1994, Wijkamp et al. 1995, Gerrin et al. 1999, Hulshof et al. 2003) while only data on *F. fusca* reproductive parameters were from Lowry et al. 1992.

Variability in reproduction of *F. occidentalis*, can be observed under many conditions. The reproduction parameters of *F. occidentalis* can be affected by host plants and plant parts (Wijkamp et al. 1995), especially pollen (Gerrin et al. 1999, Hulshof et al. 2003), and temperature (Gaum et al. 1994). Host plants can potentially exert a large influence on thrips reproduction base on host plant resistance studies (Harris et al. 2001, Messina et al. 2002, Scheirs et al. 2003). Moreover, the same host plant and temperature affected the reproductive parameters differently between different populations of *F. occidentalis* in Gaum et al. 1994 and Van Rijn et al. 1995.

This research project focuses on two species of thrips vectors, *F. occidentalis* and *F. fusca*, which are the major TSWV-vectors for crops in Georgia, and two susceptible host plants, tomato, *Lycopersicon esculentum* Mill and chickweed, *Stellaria media* (L.) Vill. over the range of temperatures from 15°C–30°C. Tomato was the first host plant on which TSWV was first

reported (Brittlebank 1919), and chickweed was reported to be the most significant host of *F. fusca* in transmission of TSWV from winter weed to peanut (Groves et al. 2002). Thus, information on thrips reproduction in both tomato and chickweed would help to understand the epidemiology of TSWV from winter weed to crop plants. In this study, we wanted to compare the reproductive potential of *F. occidentalis* and *F. fusca* between tomato and chickweed with TSWV-infection as subplot. We hypothesized that host plant species with or without TSWV-infection have no effect on net reproduction of *F. occidentalis* and *F. fusca*, however, we expected there to be a preferred host plant for reproduction. We also developed a simple model to predict the thrips vector populations in the early spring crop as part of a strategic management of thrips vectors of TSWV based on the temperature-specific reproductive performance.

Materials and Methods

Host Plants: Tomato (cv. Sunny) was seeded in pot mixture in a room maintained at 30°C with 12L:12D (light: dark), and Chickweed was seeded in pot mixture at 15°C with 12L:12D. Plants were mechanically inoculated 4 wk after seeding (with at least 2 true leaves) with either TSWV-infected or healthy tomato tissue macerated in inoculation buffer (0.1M Potassium phosphate dibasic (K_2HPO_4), 0.01M Sodium Sulfite (Na_2SO_3), 0.01M Mercaptoethanol).

TSWV inoculum were collected from field TSWV-infected tomato from the Lang farm, Tifton, GA, in May 2002 and kept frozen at -70°C. Plants were kept in the dark at 25°C for 24 h prior inoculation. After inoculation, their leaves were rinsed with water, and they were randomly assigned to selected temperature and photoperiod 1wk after inoculation. Leaf disks for thrips in each combination of temperature and photoperiod were obtained from plants in the corresponded growth chamber after 1wk acclimation for both tomato and chickweed with additional leaf disks

from tomato plants with corresponded TSWV-infection grew in a room maintained at 30°C with 12L:12D.

Thrips: Colonies of *F. occidentalis* and *F. fusca* were maintained with tomato and peanut plants, respectively. Thrips of the same age were collected and reared on green bean colonies before using in experiments. One male and one female of newly emerged adult thrips were place in each 100x15 mm plastic petri-dish (Fisherbrand®, Fisher Scientific, Pittsburgh, PA) with one 12 mm leaf disks according to the host plant treatment over moistened filter paper (90 mm Whatman® grade 1, Whatman International Ltd., Maidstone, England). One male and one female of newly emerged adult thrips were place in each 100x15 mm plastic petri-dish (Fisherbrand®, Fisher Scientific, Pittsburgh, PA) with one 12 mm leaf disks according to the host plant treatment over moistened filter paper (90 mm Whatman® grade 1, Whatman International Ltd., Maidstone, England).

Each day until a female thrips died, a new leaf disk were added for each female thrips, and the the old leaf disk was placed over moistened filter paper (15 mm Whatman® grade 1, Whatman International Ltd., Maidstone, England) in a well of 24 well cell culture cluster (Costar® 3524, Corning Incorporated, Corning, NY). All thrips were under relative humidity close to 100%. Number of eggs, first instars, second instars, prepupa, pupa, and adults in each well were counted under dissecting microscope everyday. New leaf disks with corresponding plant treatment were added every 3 days.

Temperature and photoperiod: All plants (1 week after inoculation) and petri dishes were kept at specific temperature and photoperiod in growth chambers (Percival Scientific, Boone, IA). Plants and thrips were kept under 12L:12D at the following temperatures, 15°C, 17.5°C, 20°C,

22.5°C, 25°C, 27.5°C, and 30°C, and two additional photoperiods were 6:18 and 18:6 at 20°C.

The experiment was repeated twice for each combination of temperature and photoperiod.

Statistical analysis: Number and duration of thrips in each life stage were observed to calculate reproductive parameters, net reproduction (R_0), generation time (T), and intrinsic rate of population growth (r), life-stage specific mortality. Means and standard errors were calculated by thrips species, host plant species, TSWV-infection, using PROC GLM, LSMeans (SAS version 8, SAS Institute 1999), and F-statistics were calculated using the mean square of interaction of replicate, host plant, virus and temperature as denominator.

Temperature-dependent population model

Temperature-specific and plant-specific intrinsic rates of increase were obtained from data in the reproduction of the two thrips species in the previous experiment. We used the logistic model with a regression coefficient of temperature-dependent intrinsic rate of population growth and temperature-dependent carrying capacity.

$$N = K(c)/(1+e^{-r(c)t}) ; \text{ where}$$

N: Number of individuals.

K(c): temperature-dependent carrying capacity based on temperature-specific plant growth rates of chickweed (Storkey and Cussans 2000) and tomato (Wada et al. 2001) and a maximum number of eggs/15 females per leaf disk from ovipositional preference experiment (Chapter 3).

K(c)= leaf area * leaf growth rate*maximum number of eggs per leaf disk

r(c): temperature-dependent intrinsic rate of population growth obtained from regression equation shown in Fig 7.2.

c: temperature (°C).

t: time (d)

The regression of leaf area growth rate on temperature for chickweed is $0.009t+0.017$ for temperature 5-20°C (Storkey and Cussans 2000) while the regression leaf area growth rate on temperature for tomato is $0.015t+0.023$ for temperature 5-20°C (Wada et al. 2001).

Results

Host plants significantly affected the net reproduction of *F. fusca* ($F=5.27$, $df=2,6$, $P=0.048$), but not in *F. occidentalis* ($F=1.11$, $df=2,6$, $P=0.39$) regardless of TSWV infection. *Frankliniella occidentalis* reproduced poorly on both chickweed and tomato with only the leaf disks as a food source, ($R_0=1.01$, $r=0.0005$, $T=12.2$ and $R_0=0.92$, $r=-0.006$, $T=12.7$, respectively) while *F. fusca* reproduced significantly better on chickweed ($R_0=2.51$, $r=0.0652$, $T=14.1$) than on tomato ($R_0=2.31$, $r=0.0597$, $T=14.0$) (Table 4.1). Both thrips species also had slightly higher net reproduction in non-TSWV infected plants, than TSWV-infected plants, 0.98 to 0.96 per *F. occidentalis* female, and 2.46 to 2.36 *F. fusca* per female, respectively (Table 4.1), but the effect was not significant ($F=0.054$, $df=1,6$, $P=0.824$, $F=0.11$, $df=1,6$, $P=0.748$, respectively). *Frankliniella fusca* reproduced better than *F. occidentalis* over all type of leaf disks used in this experiment (Fig. 4.1). Male-female ratios were about 3:5 for *F. fusca* and about 1:1 for *F. occidentalis* across all types of leaf disks (Table 4.1). The highest mortality rate in *F. occidentalis* occurred in eggs (0.62) while *F. fusca* had highest mortality rate in second instars (0.48) (Fig. 4.2).

Temperatures at 12L:12D significantly affected the net reproduction of both *F. occidentalis* ($F=15.45$, $df=6,6$, $P=0.002$) and *F. fusca* ($F=51.62$, $df=6,6$, $P<0.001$) (Fig. 4.3 A). Both *F. occidentalis* and *F. fusca* had highest net reproductive output at 25°C, 1.55 per female, and at 30°C, 3.23 per female, respectively, across host plant species and TSWV infection

combinations (Fig. 4.3 A). Generation times for both *F. fusca* and *F. occidentalis* were significantly shorter as temperature rose ($F=14.15$, $df=6,6$, $P=0.003$ and $F=4.64$, $df=6,6$, $P=0.042$, respectively) (Fig 4.3 B). The male to female ratio of *F. occidentalis* were closed to 1:1 in most temperatures while the male to female ratio of *F. fusca* were closed to 3:5 in most temperatures (Table 4.2).

Photoperiods at 20°C also significantly increased the net reproductions of *F. fusca* ($F=9.97$, $df=2,6$, $P=0.01$) and *F. occidentalis* ($F=4.25$, $df=2,6$, $P=0.025$, respectively) (Fig. 4.4 A). More light availability decreased the generation time of *F. fusca*, but not the generation time of *F. occidentalis* (Fig. 4.4). The male to female ratio of *F. occidentalis* increased as light hours increased while the male to female ratio of *F. fusca* decreased as light hours increased (Table 4.4).

Discussion

Frankliniella fusca reproduced better than *F. occidentalis* at all temperatures and photoperiods used in this experiment with only foliage as food source. At the low end of temperature in this experiments, *F. occidentalis* had negative population growth rate until the temperature was above 20 °C while *F. fusca* still had the positive population growth at the lowest temperature used in this experiment (15°C) (Fig 4.5 A). More light availability increased intrinsic rate of population growth of *F. fusca* but not of *F. occidentalis* (Fig 4.5 B).

Net reproduction of *F. fusca* in chickweed and tomato leaf disks, 4.03. and 2.38, respectively, at 25°C and 12L:12D from this study are comparable to peanut leaf, 4.60, at 25°C and 14L:10D (Lowry et al. 1992). However, *F. occidentalis* reproduced poorly with only leaf disks as the food source, chickweed ($R_0=1.64$ at 25°C and $R_0=1.03$ at 30°C), tomato ($R_0=1.45$ at 25°C and $R_0=1.21$ at 30°C), and peanut ($R_0=2.25$ at 25°C and $R_0=0$ at 30°C, Lowry et al. 1992)

compared a rich food source, for example, pine pollen in cucumber ($R_0=141$ at 25°C , Hulshof et al. 2003) and chrysanthemum ($R_0=99.51$ at 25°C , Katayama 1997) (Table 4.4).

The presence of pollen (Hulshof et al. 2003) or mite eggs (Trichilo and Leigh 1988) would likely increase the net reproductive output of *F. occidentalis*. The lack of pollen in early spring tomato transplants prevents tomato to be a good reproductive host as chickweed. Besides the lack of pollen as food source, the low reproductive output (R_0) and negative population growth rate (r) in *F. occidentalis* in this experiment were also strongly influenced by some of the low temperatures used in this experiment.

Although, *F. fusca* require longer generation time than *F. occidentalis*, *F. fusca* have higher population growth rate, and it is a better TSWV vector than *F. occidentalis* under only foliage as food source comparable to chickweed and early spring tomato transplant. Since both species similarly acquire TSWV (Assis et al. 2002), the higher density in one species over one another could result in more viruliferous thrips. However, *F. occidentalis* could produce more efficient TSWV vectors, though they had lower population growth rate, by reproducing higher male than female because males are better vectors than females in transmission of TSWV (Van de Wetering et al. 1998). The availability of pollen source could increase the reproductive potential of *F. occidentalis* (Hulshof et al. 2003), but chickweed under field condition will not produce flower until late spring or being induced by drought stress (Grundy and Mead 2000). One possible source of pollen for *F. occidentalis* during winter in southeastern USA is wild radish, *Raphanus raphanistrum*, (Buntin and Beshear 1995), but wild radish has low incidence of TSWV (Groves et al. 2002). Therefore, *F. occidentalis* has minor role in transmission of TSWV from winter weeds to early spring crops in southeastern USA.

Management of insect pests requires knowledge about their populations in order to justify and select suitable management tactics (Riley 1997). Insect population models allow prediction of the pest populations and subsequent determination of economic injury level (Riley 2004). Presently, several population models, such as Malthus's geometric (exponential) model, Verhulst's logistic model, and Andrewartha and Birch's multiple regression model, have been tested over wide variety of organisms as well as several insect species including thrips (Kirk 1997). Compared to empirical observations on the number of thrips per plant (Fig. 4.6 A and B), the temperature-dependence model is better in predicting the number of *F. fusca* than *F. occidentalis* on pre-blossomed tomato plants while exponential model predicted well in the period of a month. The simulated density of both thrips species during winter and spring months (Fig 4.7) shows that the densities of both thrips species in chickweed could be twice as much in May than in March, and thus higher potential risk of TSWV infection.

The availability of chickweed plants (and other winter weeds) rather than thrips population pressure on winter weeds due to reaching a carrying capacity appears to be the cause of thrips vectors of TSWV to migrate from winter weeds. Senescence of chickweed usually occurs in mid to late spring. The above models related only to foliage. The addition of pollen could greatly affect population growth of *F. occidentalis* (Gerin et al. 1999, Hulshof et al. 2003), and is the likely reason for western flower thrips being the predominant species in late spring. Tomato plants in early spring may not produce flower and pollen yet, but their foliage may contain pollen from other sources, such as pine and dogwood, to allow *F. occidentalis* to reproduce better than the condition in laboratory set up. Other factors, such as precipitation and natural enemies, may influence the population beyond a simple model can accurately predict.

Table 4.1 Average Number of thrips in each life stage per female and life table parameters, net reproduction (R_0), generation time (T), and intrinsic rate of population growth (r) of *Frankliniella fusca* and *F. occidentalis* on leaf disks of non-TSWV chickweed, TSWV-infected chickweed, non-TSWV tomato and TSWV tomato over combined temperatures and photoperiods (15, 17.5, 20, 22.5, 25, 27.5, and 30°C, at 12L:12D, 20°C at 6L:18D, and 20°C at 18L:6D) by plant species and TSWV infection.

	Plant		TSWV infection	
	Tomato	Chickweed	TSWV	Non-TSWV
<i>F. fusca</i>				
Life stage				
Egg	16.73	15.57	16.04	16.25
1 st Larva	11.89	11.70	11.68	11.91
2 nd Larva	7.72	7.92	7.73	7.91
Prepupa	4.03	4.13	4.01	4.14
Pupa	3.82	4.00	3.84	3.98
Adult	3.82	3.93	3.79	3.96
-Male	1.49	1.38	1.41	1.46
-Female	2.32	2.56	2.39	2.50
M:F ratio	0.645	0.538	0.589	0.585
R_0	2.31	2.51	2.36	2.46
T	14.0	14.1	14.3	13.8
R	0.0597	0.0652	0.0598	0.0652
<i>F. occidentalis</i>				
Life stage				
Egg	12.70	13.84	13.11	13.43
1 st Larva	4.85	5.28	5.00	5.12
2 nd Larva	3.51	3.82	3.62	3.71
Prepupa	2.08	2.26	2.14	2.20
Pupa	1.76	1.92	1.76	1.89
Adult	1.68	1.83	1.76	1.8
-Male	0.82	0.93	0.87	0.89
-Female	0.86	0.9	0.89	0.91
M:F ratio	0.9535	1.0331	0.9775	0.978
R_0	0.93	1.01	0.96	0.98
T	12.7	12.2	12.2	12.7
R	-0.006	0.0005	-0.004	-0.002

Table 4.2 Number of thrips in each life stage per female and life table parameters, net reproduction (R_0), generation time (T), and intrinsic rate of population growth (r) of *Frankliniella fusca* and *F. occidentalis* at temperatures, 15, 17.5, 20, 22.5, 25, 27.5, and 30°C, at 12L:12D on the combined leaf disks of TSWV-infected tomato, non-TSWV tomato, TSWV-infected chickweed, and non-TSWV chickweed.

Temperature (°C)	15	17.5	20	22.5	25	27.5	30
<i>F. fusca</i>							
Life stage							
Egg	7.84	10.83	13.85	13.12	23.03	21.70	21.48
1 st Larva	5.31	8.19	10.54	10.44	15.52	15.48	16.23
2 nd Larva	3.74	5.52	7.52	7.53	10.19	9.22	10.44
Prepupa	2.14	2.86	3.94	3.73	5.64	4.67	5.22
Pupa	2.11	2.69	3.85	3.67	5.34	4.38	5.02
Adult	1.86	2.69	3.85	3.67	5.34	4.38	5.02
-Male	0.71	1.00	1.26	1.03	2.14	2.00	1.78
-Female	1.14	1.69	2.59	2.64	3.20	2.38	3.24
M:F ratio	0.62	0.59	0.49	0.39	0.67	0.84	0.55
R_0	1.14	1.69	2.59	2.64	3.21	2.38	3.23
T	20.5	17.1	14.9	13.6	12.1	11.6	11.3
r	0.0066	0.0306	0.0638	0.0714	0.0963	0.0746	0.1038

F. occidentalis

Life stage							
Egg	8.57	12.34	13.69	15.80	17.57	13.78	14.09
1 st Larva	3.46	3.91	4.99	5.83	7.38	5.53	5.48
2 nd Larva	2.19	2.39	3.60	4.27	5.44	4.38	4.23
Prepupa	1.16	1.22	2.09	2.44	3.39	2.80	2.58
Pupa	0.91	0.90	1.72	1.98	3.07	2.47	2.25
Adult	0.89	0.90	1.72	1.98	3.00	2.47	2.25
-Male	0.41	0.31	0.83	0.95	1.45	1.36	1.12
-Female	0.48	0.59	0.89	1.03	1.55	1.11	1.12
M:F ratio	0.83	0.53	0.94	0.92	0.93	1.23	1.00
R_0	0.49	0.59	0.89	1.03	1.55	1.11	1.13
T	18.5	17.3	11.7	11.6	10.6	8.9	9.3
r	-0.0388	-0.0301	-0.0010	0.0027	0.0414	0.0117	0.0127

Table 4.3 Life table parameters of *Frankliniella fusca* and *F. occidentalis* at photoperiod, 6L:18D, 12L:12D and 18L:6D at 20°C on the combined leaf disks of TSWV-infected tomato, non-TSWV tomato, TSWV-infected chickweed, and non-TSWV chickweed.

Photoperiod	6:18	12:12	18:6
<i>F. fusca</i>			
Life stage			
Egg	10.27	13.85	16.31
1 st Larva	7.81	10.54	13.23
2 nd Larva	5.38	7.52	9.91
Prepupa	2.72	3.94	4.97
Pupa	2.64	3.85	4.86
Adult	2.64	3.85	4.86
-Male	0.95	1.26	1.14
-Female	1.69	2.59	3.72
M:F ratio	0.56	0.49	0.31
R_0	1.74	2.59	4.98
T	19.5	14.9	14.2
r	0.028	0.0638	0.113
<i>F. occidentalis</i>			
Life stage			
Egg	13.84	13.69	13.47
1 st Larva	4.97	4.99	4.56
2 nd Larva	3.61	3.60	3.22
Prepupa	2.02	2.09	1.78
Pupa	1.63	1.72	1.42
Adult	1.63	1.72	1.42
-Male	0.78	0.83	0.77
-Female	0.84	0.89	0.66
M:F ratio	0.93	0.94	1.17
R_0	0.59	0.89	0.51
T	17.3	11.7	12.1
r	-0.0207	-0.0010	-0.0416

Table 4.4. Comparison of net reproductive output (R_0) of *F. fusca* and *F. occidentalis* at 25°C and 30°C on various host plants and plant parts.

Thrips	Host plant	(L:D)	R_0 at 25°C	R_0 at 30°C	Reference
<i>F. fusca</i>					
	Chickweed (Leaf)	12:12	4.03	3.78	This study
	Tomato (Leaf)	12:12	2.38	2.69	This study
	Peanut (Leaf)	14:10	4.60	16.01	Lowry et al. 1992
<i>F. occidentalis</i>					
	Chickweed (Leaf)	12:12	1.64	1.03	This study
	Tomato (Leaf)	12:12	1.45	1.21	This study
	Peanut (Leaf)	14:10	2.25	0	Lowry et al. 1992
	Cucumber (Leaf)	18:6	32	N/A	Hulshof et al. 2003
	Cucumber (Leaf, pine pollen)	18:6	141	N/A	Hulshof et al. 2003
	Chrysanthemum (Leaf, petal, and pollen)	18:6	99.51	35.39	Katayama 1997

A)

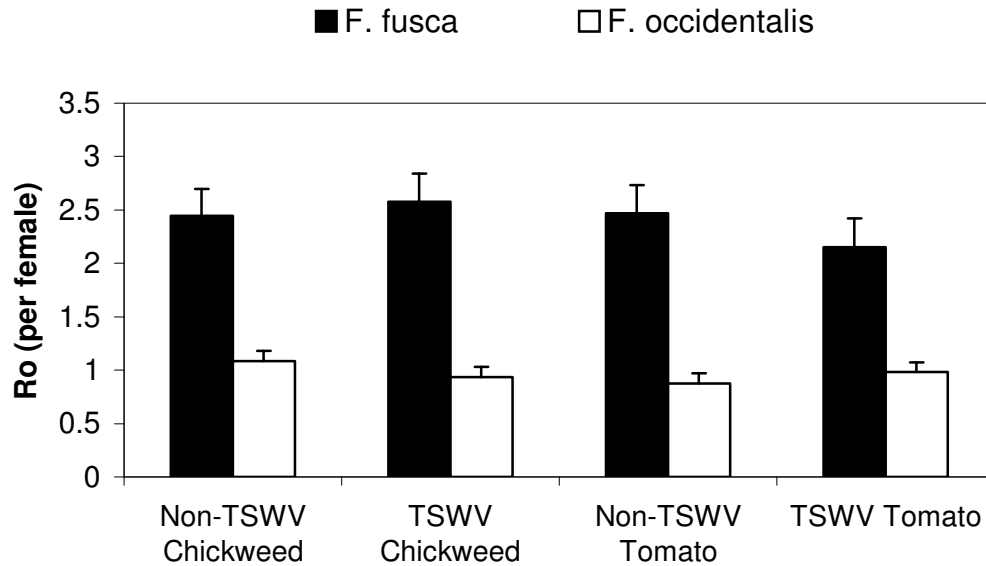


Fig. 4.1 Net reproductive rate (R_o) per female of *Frankliniella fusca* and *F. occidentalis* on leaf disks of non-TSWV chickweed, TSWV-infected chickweed, non-TSWV tomato and TSWV tomato over combined temperatures and photoperiods (15, 17.5, 20, 22.5, 25, 27.5, and 30°C, at 12L:12D, 20°C at 6L:18D, and 20°C at 18L:6D) by A) plant species and TSWV infection and by B) each type of leaf disks.

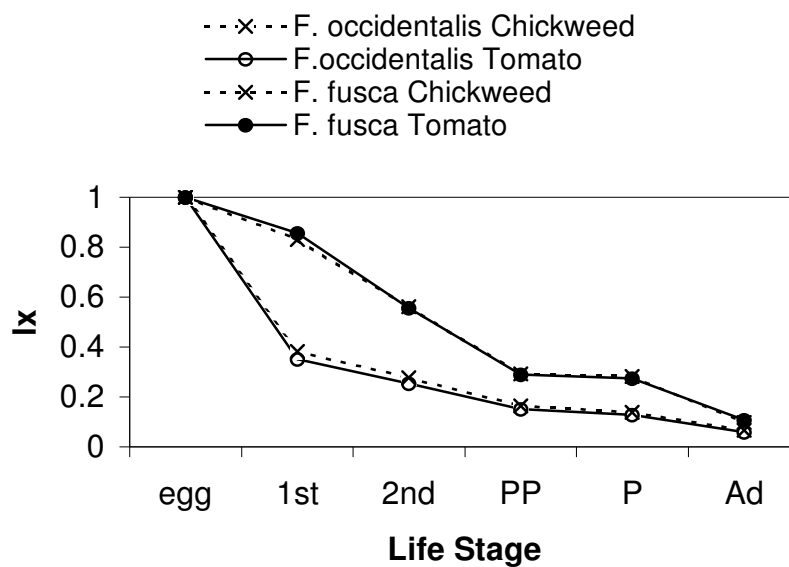
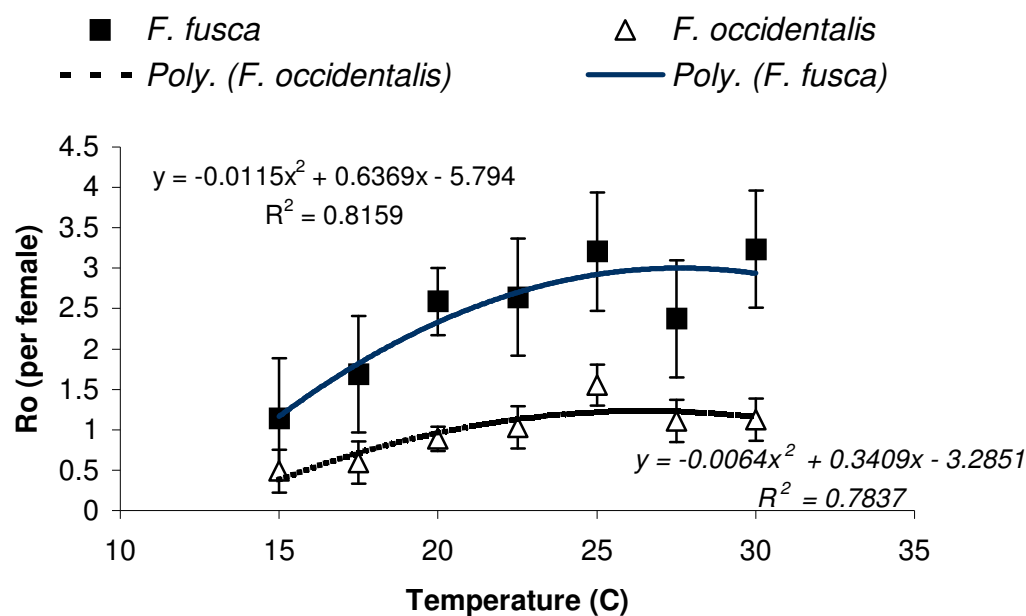


Fig 4.2 Life-stage specific survivorship (l_x) in each life stage of *Frankliniella fusca* and *F. occidentalis* on chickweed and tomato across TSWV infection and temperature combinations, 1st=1st instar, 2nd=2nd instar, PP=Prepupa, P=pupa, and Ad=Adult.

A) Net reproduction (R_0)



B) Generation time (T)

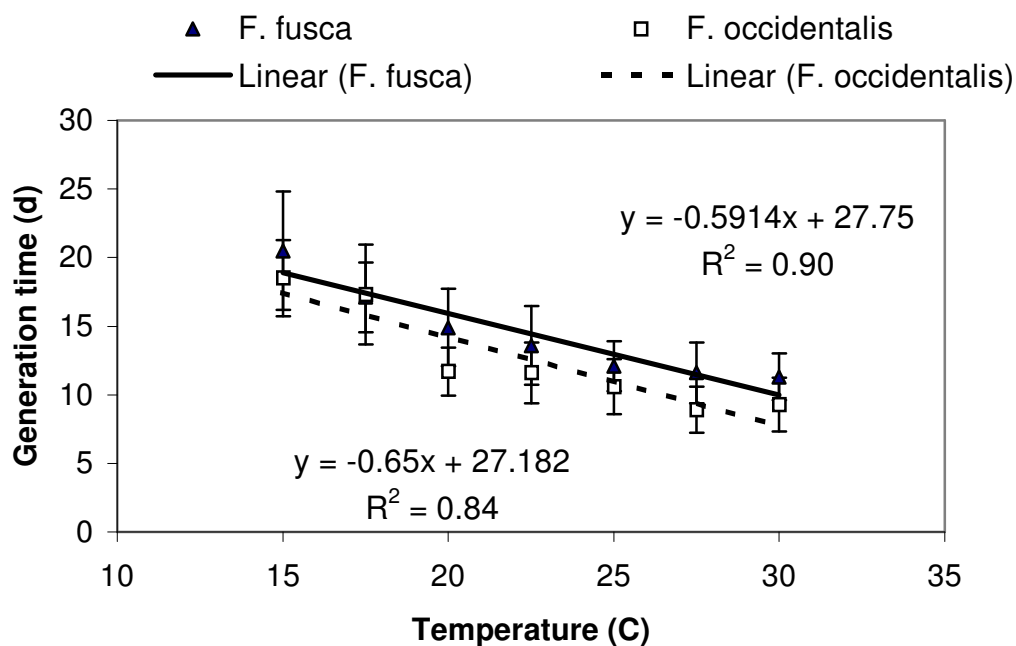
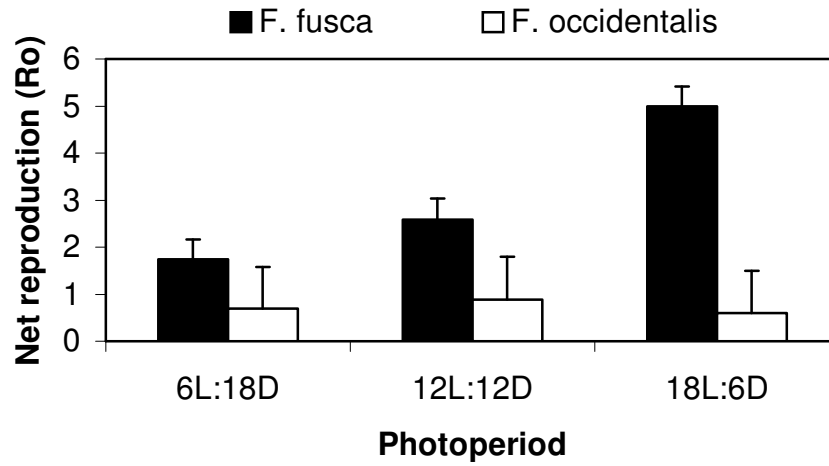


Fig. 4.3 A) Net reproductive rate (R_0) and B) generation time (T) of *Frankliniella fusca* and *F. occidentalis* across temperatures (15, 17.5, 20, 22.5, 25, 27.5, and 30°C) at 12L:12D on the combined leaf disks of TSWV-infected tomato, non-TSWV tomato, TSWV-infected chickweed, and non-TSWV chickweed.

A) Net reproduction (R_0)



B) Generation time (T)

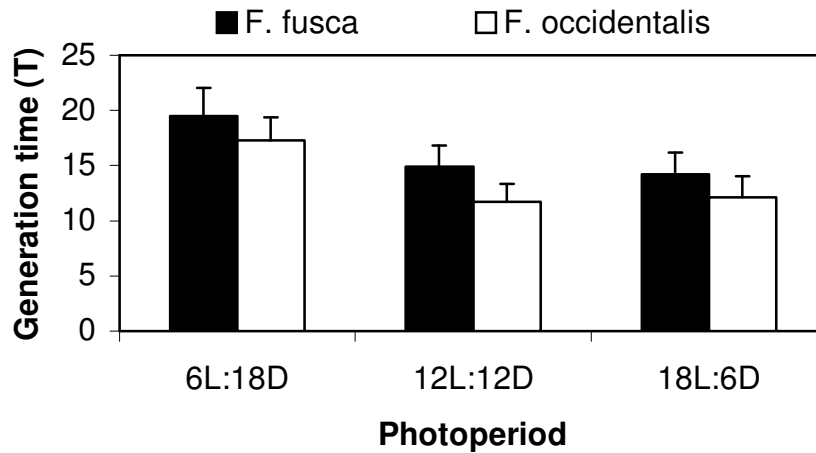
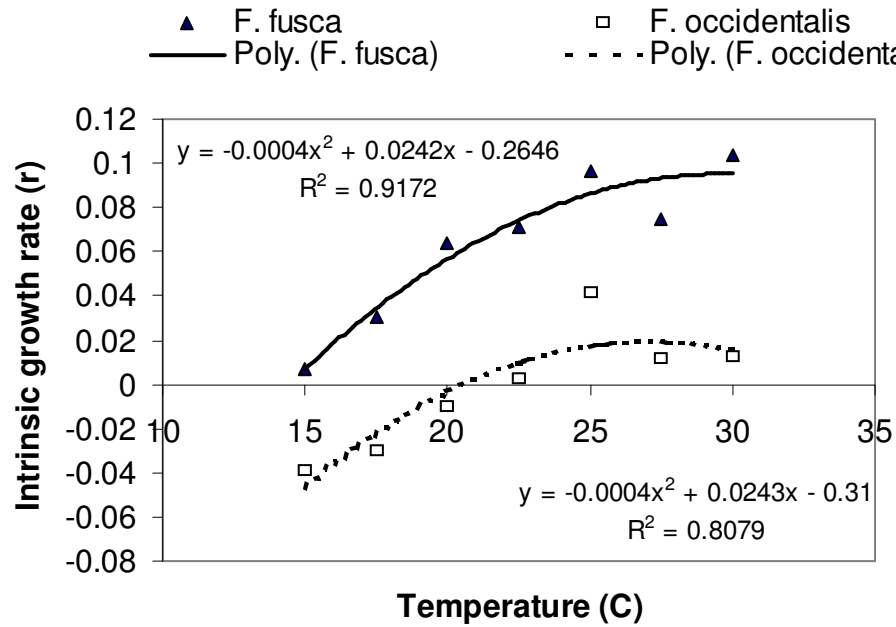


Fig. 4.4 A) Net reproductive rate (R_0) and B) generation time (T) of *Frankliniella fusca* and *F. occidentalis* across photoperiod, 6L:18D, 12L:12D and 18L:6D at 20°C on the combined leaf disks of TSWV-infected tomato, non-TSWV tomato, TSWV-infected chickweed, and non-TSWV chickweed.

A) Temperature



B) Photoperiod

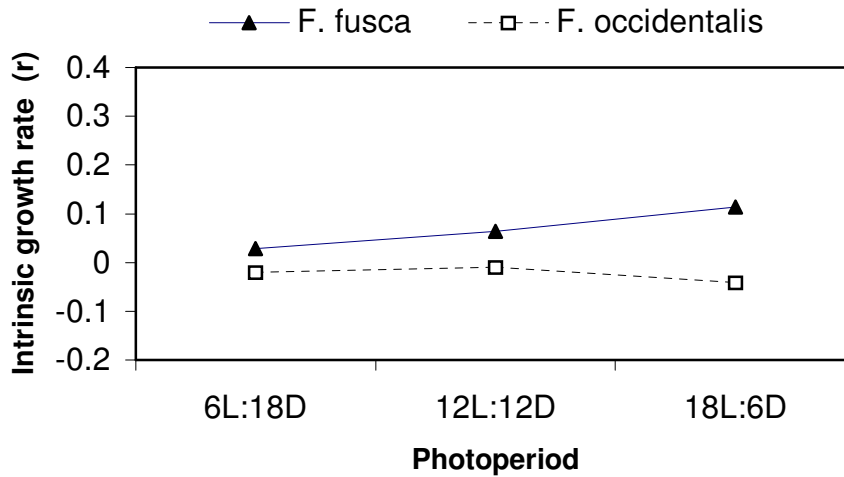
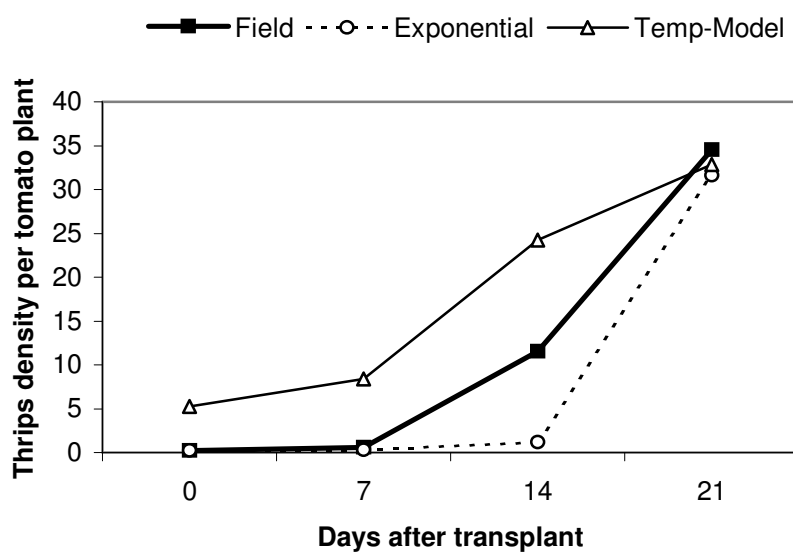


Fig. 4.5 Intrinsic rate of population growth of *Frankliniella fusca* and *F. occidentalis* by A) temperatures, 15, 17.5, 20, 22.5, 25, 27.5, and 30°C at 12L:12D and B) photoperiod, 6L:18D, 12L:12D and 18L:6D at 20°C on the combined leaf disks of TSWV-infected tomato, non-TSWV tomato, TSWV-infected chickweed, and non-TSWV chickweed.

A)



B)

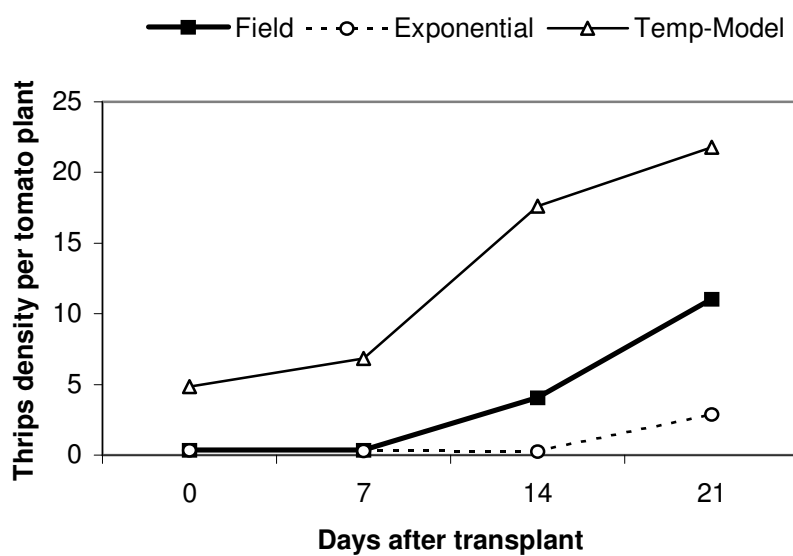


Fig 4.6. Number of **A)** *Frankliniella fusca* and **B)** *F. occidentalis* per pre-blossomed tomato plant after field transplant (4 week old plants) in March 2000, Tifton, GA (Joost and Riley 2004) comparing with number of thrips from simulated models, exponential model and temperature-dependent logistic model.

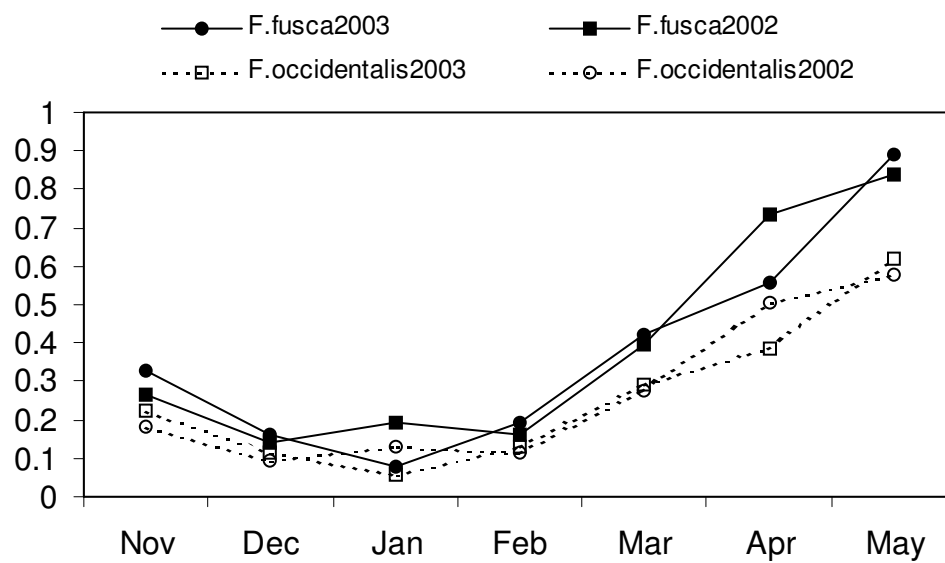


Fig 4.7 Simulated relative density of thrips expected in chickweed from November-May (available chickweed season) based on temperature data in 2002 and 2003 in Tifton, GA.

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CHAPTER 8

CONCLUSION

Biotic Factors on Thrips Reproduction

The reproduction of *Frankliniella occidentalis* and *F. fusca* were affected by plant species, but generally not by TSWV infection in host plants. *Frankliniella fusca* had a higher reproductive potential than *F. occidentalis* in these studies when only foliage was available (Chapter 4). Females of the two thrips vectors preferred to oviposit more eggs on the leaf of chickweed than tomato based on a calibrated leaf area (Fig 3.4B, Chapter 3) as well as on the standard sized leaf disk. Chickweed appeared to be the better host plant for both thrips species when only foliage was present, therefore thrips vectors likely do not migrate from chickweeds as winter reservoir to early spring tomato (pre-blossomed plants) based solely on better host plant quality. Some positive effects from TSWV infection on host plant quality may counteract the negative effects from viral multiplication in thrips vector tissues, such as deprivation of nutrients and energy that could use for reproduction to viral replication. At least, TSWV has a minimal indirect negative effects on thrips vectors through host plant quality. I only detected a 14% reduction in oviposition for *F. fusca*. The evidence from this study suggest that the migration of thrips vectors from winter reservoir weed hosts to tomato in early spring is not a factor of thrips vectors ovipositional reference on tomato foliage over chickweed foliage, but leaves one with the suspicion that the migration is rather initiated by the availability of host plants regulated by environmental factors. Simply put, when the host plant senesces, thrips will be motivated to move. In the case of chickweed, dry, hot weather in the spring will likely cause chickweed to senesce.

Abiotic Factor on Thrips Reproduction

Temperature exhibited the strongest influence on thrips reproduction over host plant, photoperiod, and TSWV infection in this research. Both thrips species had higher reproductive rate at temperature between 25-30°C, and had the minimum temperatures for population growth between 10-13°C when their diets consisted of only foliage. The rising of temperature in early spring increases the reproductive potential of both thrips species and it coincides with the decline of chickweed due to the emergence of better competitive weeds. The faster population growth and the reduced carrying capacity from the disappearance of chickweed over the course of spring promote the migration of thrips, included viruliferous thrips, to early spring crops, such as tomato, even though tomato foliage does not serve as better host than chickweed. As the temperature rises over the course of summer, the temperature higher than optimum temperature for population growth may cause the reduction of thrips populations to be low during fall tomato growing season.

The changes in temperature or photoperiod did not change the ovipositional preference of the thrips from chickweed over tomato, however, the pollen effects on *F. fusca* reproduction has not been documented extensively has been done for as *F. occidentalis*. Also, the quality of pollen from different host plants reportedly vary from plant species to other species, and apparently significantly affected the reproductive rate of *F. occidentalis* (Hulshof et al. 2003). Temperature and photoperiod affect the germination and growth of plants (Stokey and Cussan 2000), and they could as well alter the quality of the plant or the availability of pollen.

Implication to TSWV management

The management of important winter reservoir weeds, such as chickweed, requires the environmental data and model to predict the emergence as well as senescence of the weed host.

This will affect the thrips populations since the population growth of thrips is primarily based on temperature as well as host plant availability. The weather as well as the level of weed reservoirs along with the monitoring of thrips populations is potentially an important tool in TSWV management. These data could help in avoiding the peak in thrips populations and well as selection control tactics and application time (at the most critical time frame) to impact yield in the most beneficial manner.

The immediate application of my model is to incorporating the temperature monitoring to predict the populations level of thrips vector or potential TSWV risk in the spring growing season. Other factors, such as precipitation and natural enemies, may affect the population levels and should be included if these factors allow the model to be more precise.

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APPENDIX A

PROTOCOLS RELATED TO EXPERIMENTS IN CHAPTER 3-6

Protocol for Leaf Staining with Lactophenol Acid Fuchsin (Chapter 3)

1. Wash leaves with 75% alcohol in self-sealed plastic bag and shake gently.
2. Remove thrips, if any, and record number by adult and immature.
3. In beaker, add the decolorize mixture (2:1:1 v/v/v of 75% alcohol: glacial acetic acid: 10% lactic acid).
4. Add leaves to beaker in water bath at 60-70°C in fumehood for 10 minutes.
5. Allow leaves to cool in decolorize mixture until leaves clear and leaves can be left in the solution indefinitely until clear.
6. Remove leaves from beaker put in a self-sealed plastic bag, add lactophenol acid fuchsin, and shake gently and leave for 24-48 hours.
7. (Optional counter stain) repeat step 6. replaced lactophenol acid fuchsin with lactophenol cotton blue.
8. Examine stained under dissecting microscope for any feeding and oviposition (red circular ring about 1 mm) sites.

Recipe for Lactophenol solution.

1. Dissolve 25 g phenol in 50 mL water .
2. Add 25 mL lactic acid.
3. Add 50 mL glycerine.
4. Store away from light.

Recipe for Lactophenol Acid Fuchsin and Lactophenol Cotton Blue

1. Dissolve 1 g of acid fuchsin or cotton blue to 100 mL lactophenol.
2. Dilute 5 mL of the solution from step 1. to 100 mL with lactophenol before use.

Safety precaution

Wearing gloves when handling phenol, acetic acid, and lactic acid.

Working in fumehood when mix the solution and decolorize the leaves.

Protocol for Thrips Rearing on Leaf Disks (Chapter 4, 5, and 6).

Host Plants: Tomato (cv. Sunny, Agrow Seed Co., Kalamazoo, MI) was seeded in pot mixture in a room maintained at 30°C with 12L:12D (light: dark), and Chickweed (Thyme Garden Herb Company, Alsea, OR) was seeded in pot mixture at 15°C with 12L:12D.

TSWV-Inoculation: Plants were mechanically inoculated when they were 4 wk after seeding (with at least 2 true leaves) with either TSWV-infected or healthy tomato tissue macerated in inoculation buffer (0.1M Potassium phosphate dibasic (K_2HPO_4), 0.01M Sodium Sulfite (Na_2SO_3), 0.01M Mercaptoethanol) over leaf surface that was lightly dusted of carborundum powder. TSWV inoculum was collected from field TSWV-infected tomato from the Lang farm, Tifton, GA, in May 2002 and kept frozen at -70°C. Plants were kept in dark at 25°C for 24h prior inoculation. After inoculation, their leaves were rinsed with water, and they were randomly assigned to selected temperature and photoperiod 1 wk after inoculation.

Thrips Source: Colonies of *F. occidentalis* and *F. fusca* were maintained on green bean in plastic cups. *Frankliniella occidentalis* were originally collected from wild radish flowers in November, 2000, Tifton, GA, and *F. fusca* were originally collected from peanut plants in May 2000, Tifton, GA. Natural populations of *F. occidentalis* (from tomato blossoms (summer) and wild radish (winter)) and of *F. fusca* (from tomato plants and peanut plants) were occasionally added to the colonies to maintain diversity.

Leaf Disks: Leaf disks for thrips in each combination of temperature and photoperiod were obtained from plants in the corresponded growth chamber after 1 wk acclimation for both tomato and chickweed with additional leaf disks from tomato plants with corresponded TSWV-infection grew in 30°C with 12L:12D room. A 12 mm brass hole puncher was pressed over leaf bigger than the puncher to create leaf disks, and if a leaf, normally chickweed, did not fit the punching area but had comparable leaf area, it was used as a whole leaf.

Humidity control -moistened filter papers: For adult thrips arena, a filter paper (90 mm Whatman® grade 1, Whatman International Ltd., Maidstone, England) was placed inside the larger piece of a 100x15mm plastic petri-dish (Fisherbrand®, Fisher Scientific, Pittsburgh, PA). For immature arena, a filter paper (15 mm Whatman® grade 1, Whatman International Ltd., Maidstone, England) was placed in a well of 24-well cell culture cluster (Costar® 3524, Corning Incorporated, Corning, NY). Water was added to over-saturate filter papers, and excess water was removed by flipping over the plate or dish while the moistened filter papers remained at the bottom of the plate or dish. A well-moistened filter paper can hold and seal the two pieces of a 100x15mm plastic petri-dish. Water was added every 2-3 days to replace the evaporate water and excess water was removed by using a Pasteur pipette.

Ovipositional preference study: Five male and fifteen females of newly emerged adult thrips were placed using a moistened fine brush in a 100x15 mm plastic petri-dish with four equidistant 12 mm leaf disks according to the host plant treatments over moistened 90mm filter paper. The plant treatments were consisted of the combination of non-infected tomato, non-infected chickweed, TSWV-infected tomato, and TSWV-infected chickweed. One-choice treatments, 4 treatments per replicate, were consisted of four leaf disks of the same plant specie and the presence of TSWV. Two-choice treatments, 6 treatments per replicate, were consisted of

two leaf disks of the same plant species and the presence of TSWV and two plants with the one other of the remaining three combinations. Four-choice treatment, 1 treatment per replicate, was consisted of four leaf disks from each combination of plant specie and the presence of TSWV. After 7 d, eggs on each leaf disk were counted under dissecting microscope, and the leaf disks were placed in 24-well plate to observe any immature emerge from eggs.

Life table study: One male and one female of newly emerged adult thrips were place in each 100x15mm plastic petri-dish with one 12 mm leaf disks according to the host plant treatment over 90mm moistened filter paper. Each day until a female thrips died, a new leaf disk were added, and the old leaf disk was placed over moistened 15 mm filter paper in a well of 24-well plate. Number of eggs, first instars, second instars, prepupa, pupa, and adults in each well were counted under dissecting microscope everyday. When the immatures reached pupal stage, the plate was covered with plastic wrap underneath the lid to prevent the movement of adults between wells. New leaf disks with corresponded plant treatment were added every 3 days. When immatures were over 5 individuals per leaf disk, they were separated into new leaf disks with less than 5 individuals per leaf disk.

Temperature and photoperiod: All plants (1 week after inoculation) and petri dishes were kept at specific temperature and photoperiod in growth chambers (Percival Scientific, Boone, IA). Plants and thrips were kept under 12L:12D at the following temperatures, 15°C, 17.5°C, 20°C, 22.5°C, 25°C, 27.5°C, and 30°C, and two additional photoperiods were 6:18 and 18:6 at 20°C. The experiment was repeated twice for each combination of temperature and photoperiod.

APPENDIX B

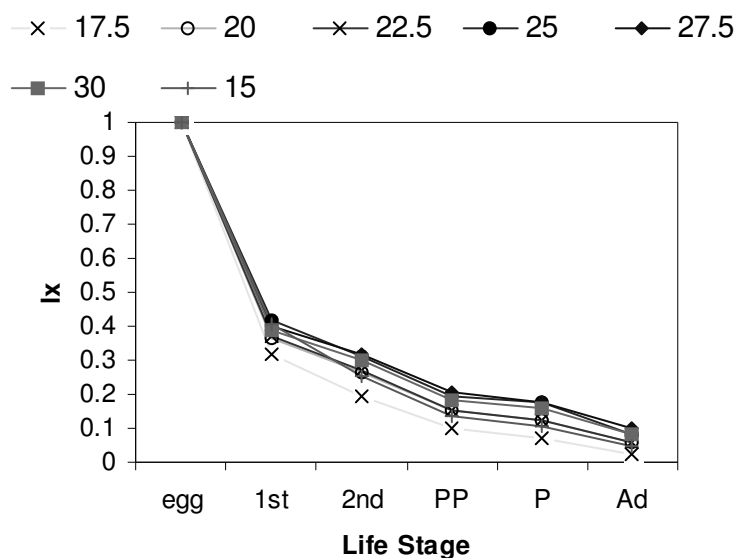
POPULATION DYNAMIC OF THRIPS OVER INFECTED AND NON-INFECTED FIELD

TOMATO

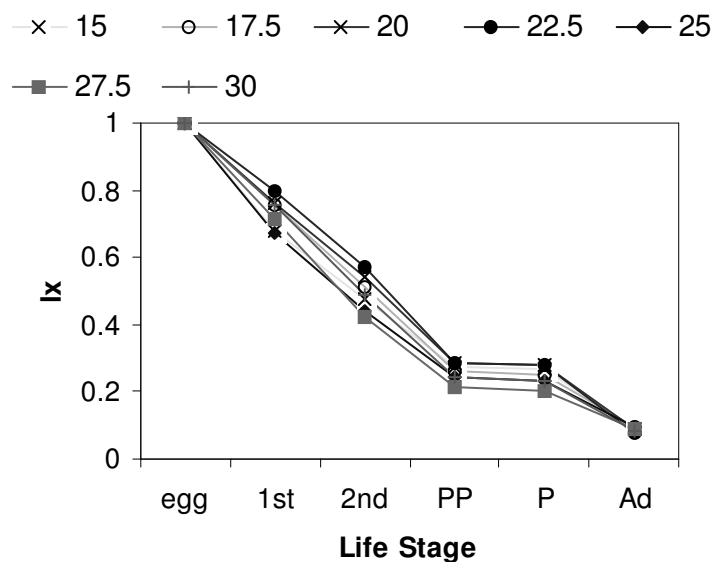
Ovipositional preference of *Frankliniella occidentalis* (Pergande) (western flower thrips) and *F. fusca* (Hinds) (tobacco thrips) were determined in field sampling using beating cup with TSWV-infected and non-infected tomato (*Lycopersicon esculentum* Mill cv. Sunny Hybrid) at different ages (pre-blossomed and blossomed) in May-July 2001, May-July 2002, and March-June 2003. Only 2003 test were successful since the field tests in 2001 and 2002 were failed to detect any significant density of thrips and were infested with whiteflies and tobacco hornworm, respectively, due to the necessity of non-insecticide treatment. In 2003 field test, the majority of thrips, 97%, were *F. occidentalis* followed by *F. fusca* and *F. tritici*, and there were 0.3 ± 0.07 eggs per leaflet per plant per week from April-May. There were no significant difference in the number of eggs in leaflet between TSWV infected and non-TSWV infected plants in any field test.

APPENDIX C

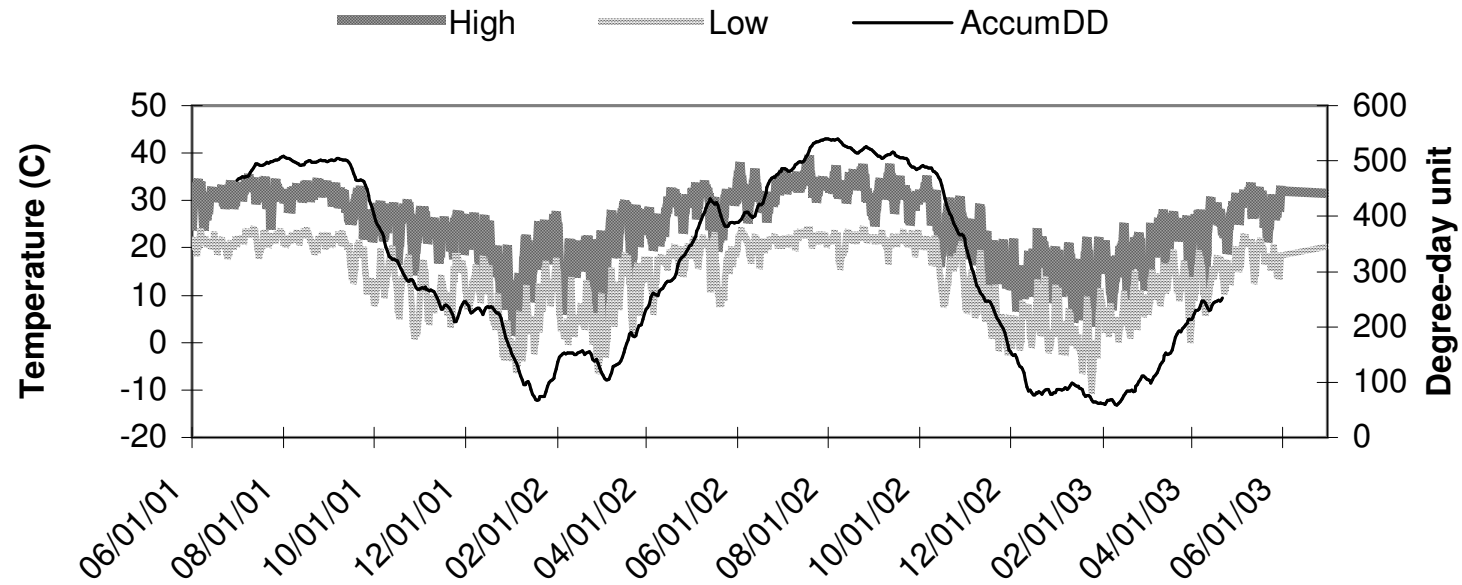
GRAPHS AND TABLES NOT PRESENTED IN THE CHAPTERS



Apd-C.1 Life-stage specific survivorship (lx) in each life stage of *Frankliniella occidentalis* at temperatures across host plant species and TSWV infection combinations, 1st=1st instar, 2nd=2nd instar, PP=Prepupa, P=pupa, and Ad=Adult.



Apd-C.2 Life-stage specific survivorship (lx) in each life stage of *Frankliniella fusca* at temperatures across host plant species and TSWV infection combinations, 1st=1st instar, 2nd=2nd instar, PP=Prepupa, P=pupa, and Ad=Adult.



Apd-C 3. Daily maximum (High) and minimum (Low) temperature, and monthly accumulated degree-day (AccumDD) from 6/01/01-6/01/03 in Tifton, GA.

BIOGRAPHY

Chatchawan Chaisuekul was born on January, 30 1976 in Bangkok, Thailand. He is a youngest son of Boonchoo and Wandee Chaisuekul. He received elementary education from Phayathai and secondary education from Suankularb Wittayalai in Bangkok. After finished high school in 1993, he attended Chulalongkorn University at Faculty of Science where he was awarded a scholarship from the Development and Promotion of Science and Technology Talent Project, and later to continued his undergraduate program at University of Delaware in 1994.

After received Bachelor of Arts in biology from University of Delaware in 1998, he attended a graduate program in entomology at University of Georgia. He was awarded Master of Science in Entomology in 2000 with the thesis title of ‘Tomato plant age effects on the transmission of *Tomato spotted wilt virus* and insecticide inhibition of the thrips-vector feeding’ and continued his Ph.D.’s research on oviposition preference and reproduction of thrips vectors of *Tomato spotted wilt virus* under the guidance of Dr. David G. Riley.