ABSTRACT

BEAUDOIN, AMANDA LYNN PARODI. Temporal and Spatial Patterns of Thrips Dispersal in Relation to the Epidemiology of *Tomato Spotted Wilt Virus*. (Under the direction of George G. Kennedy and Rick Brandenburg.)

Tomato spotted wilt virus (family Bunyaviridae, genus *Tospovirus*, TSWV) is the causative agent of the disease, tomato spotted wilt (TSW), which affects many crops including tomato, pepper, peanut, and tobacco. The tobacco thrips, *Frankliniella fusca*, is considered the most important early season vector in North Carolina, and the western flower thrips, *F. occidentalis*, is considered an important vector when found in abundance. *F. fusca* and *F. occidentalis* disperse from winter annual weeds to summer annual weeds and crops in spring. Regional temperature and rain can explain the majority of variation in numbers of thrips captured on sticky traps; however, the numbers of thrips captured from nearby farms that experience similar weather are often variable in magnitude, and model validation attempts for individual farms yielded inadequate predictions. The importance of field and field margin characteristics were studied to better understand thrips and TSWV dynamics on a farm scale. Specifically, the effect of pepper plant age on TSWV prevalence, the effect of weed management on timing and magnitude of *F. fusca* dispersal, the relationship between *F. fusca* captures and TSW prevalence with distance to weedy margins, and the plausibility of secondary spread of TSW within tomato and pepper fields were studied. Based on regression models of percentage of pepper plants infected with increasing age, the predicted percentage of infected plants was reduced by 50% within nine days post transplant compared to plants infected at transplant, indicating that the timing of TSWV spread to pepper relative to plant age is critical. Management type and timing of winter weeds affect *F. fusca* dispersal magnitude and duration. Herbicide application increased *F. fusca* dispersal compared to

untreated plots, but disking did not increase dispersal. Furthermore, more *F. fusca* dispersed from weeds that were managed at a late date compared to an untreated check, and elevated dispersals lasted longer from late managed weeds than from early managed weeds. Using a grid of sticky traps over bare soil, it was determined that *F. fusca* can disperse for hundreds of meters from weedy margins, the closest source of *F. fusca*. It was hypothesized that a greater abundance of *F. fusca* and TSW prevalence would be observed with increasing proximity to natural weed hosts; however, increasing numbers of captured *F. fusca* and increasing TSW prevalence with increasing distance from weeds were observed. Clustering of *F. fusca* captured and TSW prevalence was observed in all fields and generally reflected relationships observed using regression analysis. Sticky trap, foliage, and blossom data from tomato and pepper fields indicate that *F. fusca* are transient and do not establish resident populations within the fields, but *F. occidentalis* does colonize at least some fields of both crops. Transmission assays using thrips vectors collected from within the field indicate that some *F. occidentalis* acquire TSWV from infected plants within the field and are competent vectors, potentially contributing to secondary spread. Regression models for tomato provided evidence that secondary spread of TSWV occurs. Overall, results indicate that management of neighboring weed hosts of thrips vectors is unlikely to prevent TSW primary spread due to the ability of *F. fusca* to move long distances across a field, but care can be taken not to increase thrips and TSWV exposure, especially if management would increase thrips dispersal when plants susceptible to TSWV have been recently transplanted. Additional work to understand whether controlling resident populations of *F. occidentalis* in tomato and pepper fields reduces late season TSW and increases marketable yield is warranted.

Temporal and Spatial Patterns of Thrips Dispersal in Relation to the Epidemiology of *Tomato Spotted Wilt Virus*

by
Amanda Lynn Parodi Beaudoin

A dissertation submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Entomology

Raleigh, North Carolina

2011

APPROVED BY:

_____	_____
George G. Kennedy Committee Chair	Rick Brandenburg Committee Co-chair
_____	_____
Frank Louws	David Jordan

DEDICATION

To my best friend and husband, Billy:

This work would not have been possible without your support and encouragement.

Thank you for cheering me along my journey. I love you.

To my parents, Herman and Violet Parodi:

You taught me to work hard, aim high, and to find the fun and humor in all that I do.

To my buddy, Carol Berger:

You are a great listener, a patient teacher, and a compassionate friend.

BIOGRAPHY

Amanda Lynn Parodi Beaudoin was born in Allentown, Pennsylvania. She lived in Pennsylvania for 14 years before moving to Florida, where she graduated from Deltona High School. She was accepted into the Park Scholarship program and completed a B.S. in Geology with honors at North Carolina State University. Although she continues to love all natural sciences, Amanda found a love for entomology after working as a laboratory assistant for Dr. George Kennedy. She pursued a PhD in entomology as Dr. Kennedy's student.

ACKNOWLEDGMENTS

The author thanks her advisor, Dr. George Kennedy, for his time and guidance in the preparation of this work. She is honored to work with someone of his talent both as a researcher and mentor, and she will always be grateful for the positive influence he has had on her life. The author also thanks her committee members, Drs. Rick Brandenburg, Frank Louws, and David Jordan for their opinions and support. Invaluable statistical analysis suggestions were provided by Drs. Cavell Brownie, Consuelo Arellano, and Tom Chappell. The author thanks the many people who provided technical support in the field, laboratory, and greenhouse, especially Carol Berger, Daniel Grist, Kevin Langdon, and Kevin Littlejohn. The author extends particular thanks to the North Carolina growers who allowed her to use their fields for sampling and data collection. Finally, the author would like to thank her many family and friends that provided encouragement throughout her Ph.D. program. Thanks to all of you!

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 3: SPATIAL PATTERNS OF *FRANKLINIELLA FUSCA* (THYSANOPTERA: THRIPIDAE) CAPTURES AND *TOMATO SPOTTED WILT VIRUS* PREVALENCE IN RELATION TO WEEDY FIELD MARGINS

CHAPTER 4: ASSESSMENT OF THE POTENTIAL FOR SECONDARY SPREAD OF *TOMATO SPOTTED WILT VIRUS* IN TOMATO AND PEPPER FIELDS BASED ON IN-DEPTH OBSERVATIONS OF *FRANKLINIELLA FUSCA* (HINDS) AND *F. OCCIDENTALIS* (PERGANDE) THROUGHOUT THE GROWING SEASON

Introduction

Thrips are economically important agricultural pests worldwide, which cause both direct and indirect crop damage. Young tomato (*Solanum lycopersicum* L.), pepper (*Capsicum annuum* L.), peanut (*Arachis hypogea* L.), and tobacco (*Nicotiana tabacum* L.) plants can be damaged directly through feeding or indirectly via transmission of *tomato spotted wilt tospovirus* (TSWV) (Barbour and Brandenburg 1994, Brecke et al. 1996, Cho et al. 1995, Eckel et al. 1996, Gitaitis et al. 1998, Groves et al. 2003, McPherson et al. 1999, Nault et al. 2003). Thrips are the exclusive vectors of *tomato spotted wilt virus* (Family Bunyaviridae, Genus *Tospovirus*, TSWV), and TSWV can cause annual crop losses of over $1 billion worldwide (Goldbach and Peters 1994) and losses across the southeastern United States over $100 million (Pappu 1997). At least eight species of thrips are documented TSWV vectors, and the western flower thrips, *Frankliniella occidentalis* (Pergande), is considered the most important TSWV vector worldwide (Whitfield et al. 2005, German et al. 1992). In North Carolina, the tobacco thrips, *F. fusca* (Hinds), is considered an important vector, especially early in the growing season, and *F. occidentalis* is typically patchy in distribution and considered a major problem only situationally in North Carolina (Eckel et al. 1996, Groves et al. 2003).

F. fusca and *F. occidentalis* can be found feeding on over 900 plant species across more than 80 plant families. Because *F. fusca* and *F. occidentalis* commonly live on summer and winter annual host plants, two seasonal dispersals are typically observed as hosts begin to senesce and thrips disperse to new hosts. Populations of thrips and TSWV inoculum increase on winter annual hosts in late winter and spring and disperse to summer hosts and

crops beginning in spring. In North Carolina, *F. fusca* and *F. occidentalis* spring dispersals typically peak in late May or June (Eckel et al. 1996, Groves et al. 2003, Morsello et al. 2009). In fall, thrips disperse from summer annual and perennial hosts to winter annual and perennial hosts where they overwinter (Chamberlin et al. 1992, Cho et al. 1995, Groves et al. 2001, 2002).

F. fusca and *F. occidentalis* can only acquire TSWV as first instar larvae, and TSWV is passed transstadially. Infected adults can transmit TSWV for the remainder of their lives, but infection is not passed transovarially (Linford 1962, Sakimura 1962, van de Wetering et al. 1996). Because TSWV can only be acquired by first instar thrips and the mobility of larvae is limited, thrips must hatch and feed on TSWV-infected plants to become viruliferous.

Management of TSWV and thrips vectors has proven challenging. Although insecticides effective on both *F. fusca* and *F. occidentalis* are available, thrips are able to transmit TSWV before the insecticides kill the insects. In addition, thrips exhibit thigmotactic behavior, and the tendency to dwell in the nooks of plants means that even if insecticide is used, many of the places the thrips prefer to occupy are not reached by insecticide. Elimination of inoculum sources is an alternative plant disease control strategy. Endeavors to study which summer and winter annual weeds are most important to the cycle of TSWV spread led to the realization that the virus and thrips weed hosts are so common in the North Carolina farmscape that elimination of these hosts is unrealistic (Groves et al. 2001, 2002, 2003; Kahn et al. 2005).

Recently, analysis relating thrips captured on sticky traps with various climate parameters demonstrated the regional importance of weather on thrips dispersal in North Carolina and Virginia. Degree day accumulation can be used to predict turnover of *F. fusca* and *F. occidentalis* generations (Lowry et al. 1992). In general, regional dispersal patterns of *F. fusca* can be described using local temperature and rainfall data (Morsello et al. 2008, 2009, 2010). However, the magnitude and date of peak *F. fusca* captures on sticky traps for individual farms was variable, and the models did not accurately predict thrips captures on sticky traps for individual farms. This indicates that additional parameters are required to predict magnitude of thrips present at a specific farm, and it is likely that local farm practices influence thrips dispersal patterns and subsequent sticky trap captures. The objective of this work was to understand the importance of field and field margin characteristics as related to thrips and TSWV dynamics on a farm scale. Specifically, the effect of pepper plant age on TSWV prevalence, the effect of weed management on timing and magnitude of *F. fusca* dispersal, the relationship between *F. fusca* captures and TSW prevalence with distance to weedy margins, and the plausibility of secondary spread of TSW within tomato and pepper fields were studied.

References Cited

Barbour, J. D and R. L. Brandenburg. 1994. Vernal infusion of thrips into North Carolina peanut fields. J. Econ. Entomol. 87: 446-451.

Breke, B. J., J. E. Funderburk, I. D. Teare, and D. W. Gorbet. 1996. Interaction of early-season herbicide injury, tobacco thrips injury, and cultivar on peanut. Agron. J. 88: 14-18.

Chamberlin, J. R., J. W. Todd, R. J. Beshear, A. K. Culbreath, and J. W. Demski. 1992. Overwintering hosts and wingform of thrips, *Frankliniella* spp., in Georgia (Thysanoptera: Thripidae): implications for management of spotted wilt disease. Environ. Entomol. 21: 121-128.

Cho, K. C., S. Eckel, J. F. Walgenbach, and G. G. Kennedy. 1995. Overwintering of thrips (Thysanoptera: Thripidae) in North Carolina. Environ. Entomol. 24: 58-67.

Eckel, C. S., K. Cho, J. F. Walgenbach, G. G. Kennedy, and J. W. Moyer. 1996. Variation in thrips species composition in field crops and implications for tomato spotted wilt epidemiology in North Carolina. Entomol. Exp. Appl. 78: 19-29.

German, T. L., D. E. Ullman, and J. W. Moyer. 1992. *Tospoviruses*: diagnosis, molecular biology, phylogeny, and vector relationships. Annu. Rev. Phytopathol. 30: 315-348.

Gitaitis, R. D., C. C. Dowler, and R. B. Chalfant. 1998. Epidemiology of tomato spotted wilt in pepper and tomato in southern Georgia. Plant Dis. 83: 752-756.

Goldbach, R. and D. Peters. 1994. Possible causes of the emergence of tospovirus diseases. Virology. 5: 113-120.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2001. Overwintering of *Frankliniella fusca* (Thysanoptera: Thripidae) on winter annual weeds infested with tomato spotted wilt virus and patterns of virus movement between susceptible hosts. Phytopathol. 91: 891-899.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2002. The role of weed hosts and tobacco thrips, *Frankliniella fusca*, in the epidemiology of tomato spotted wilt virus. Plant Dis. 86: 573-582.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2003. Seasonal dispersal patterns of *Frankliniella fusca* (Thysanoptera: Thripidae) and tomato spotted wilt virus occurrence in central and eastern North Carolina. J. Econ. Entomol. 96: 1-11.

Kahn, N. D., J. F. Walgenbach, and G. G. Kennedy. 2005. Summer weeds as hosts for *Frankliniella occidentalis* and *Frankliniella fusca* (Thysanoptera: Thripidae) and as reservoirs for tomato spotted wilt tospovirus in North Carolina. J. Econ. Entomol. 98: 1810 – 1815.

Linford, M. B. 1962. Transmission of the pineapple yellow-spot virus by *Thrips tabaci*, pp. 301-324. *In* K. Maramorosch (ed.) Biological transmission of disease agents: symposium held under the auspices of the Entomological Society of America: Atlantic City, 1960. Academic Press, New York.

Lowry, V. K., J. W. Smith, and F. L. Mitchell. 1992. Life-fertility tables for *Frankliniella fusca* (Hinds) and *F. occidentalis* (Pergande) (Thysanoptera: Thripidae) on peanut. Ann. Entomol. Soc. Am. 85: 744-754.

McPherson, R. M., H. R. Pappu, and D. C. Jones. 1999. Occurrence of five thrips species on flue-cured tobacco and impact on spotted wilt disease incidence in Georgia. Plant Dis. 83: 765-767.

Morsello, S. C., A. L. P. Beaudoin, R. L. Groves, B. A. Nault, and G. G. Kennedy. 2010. The influence of temperature and precipitation on spring dispersal of *Frankliniella fusca* changes as the season progresses. Entomologia Experimentalis et Applicata. 134: 260-271.

Morsello, S. C. and G. G. Kennedy. 2009. Spring temperature and precipitation affect tobacco thrips, *Frankliniella fusca,* population growth and tomato spotted wilt virus spread within patches of the winter annual weed *Stellaria media.* Entomol. Exp. Appl. 130: 138-148.

Morsello, S. C., R. L. Groves, B. A. Nault, and G. G. Kennedy. 2008. Temperature and precipitation affect seasonal patterns of dispersing tobacco thrips, *Frankliniella fusca*, and onion thrips, *Thrips tabaci* (Thysanoptera: Thripidae) caught on sticky traps. Environ. Entomol. 37: 79-86.

Nault, B.A., J. Speese III, D. Jolly, and R. L. Groves. 2003. Seasonal patterns of adult thrips dispersal and implications for management in eastern Virginia tomato fields. Crop Prot. 22: 505-512.

Pappu, H. R. 1997. Managing tospoviruses through biotechnology: Progress and prospects. Biotechnology and Development Monitor. 32: 1417-1421.

Sakimura, K. 1962. The present status of thrips-borne viruses, pp. 33-40. *In* K. Maramorosch (ed.) Biological transmission of disease agents: symposium held under the auspices of the Entomological Society of America: Atlantic City, 1960. Academic Press, New York.

van de Wetering, F., R. Goldbach, and D. Peters. 1996. Tomato spotted wilt tospovirus ingestion by first instar larvae of *Frankliniella occidentalis* is a prerequisite for transmission. Phytopathol. 86(9): 900-905.

Whitfield, A.E., D.E. Ullman, and T.L. German. 2005. Tospovirus-thrips interactions. *Annu. Rev. Phytopathol.* 43: 459-489.

CHAPTER 1

Bell and Banana Pepper Exhibit Mature-plant Resistance to Tomato Spotted Wilt Tospovirus Transmitted by *Frankliniella fusca* (Thysanoptera: Thripidae)

Text as published.

Beaudoin, A. L. P., N. D. Kahn and G. G. Kennedy. 2009. Bell and Banana Pepper Exhibit Mature-plant Resistance to Tomato Spotted Wilt Tospovirus Transmitted by *Frankliniella fusca* (Thysanoptera: Thripidae). J. Econ. Entomol. 102: 30-35.

Abstract

Tomato spotted wilt virus (family *Bunyaviridae*, genus *Tospovirus*, TSWV) causes annual economic losses in pepper, *Capsicum annuum* L., across the southern United States and is transmitted by several species of thrips including the tobacco thrips, *Frankliniella fusca* (Hinds). Reduced virus transmission and symptom severity as plant age increases is known as mature-plant resistance. TSWV transmission to pepper plants was examined in three and four age classes in field and greenhouse trials, respectively. In the field trial, Camelot bell pepper plants were exposed to potentially viruliferous *F. fusca* 37, 51, or 65 days post sowing. Two greenhouse trials of Camelot bell and one trial each of Bounty and Pageant banana pepper plants were exposed to potentially viruliferous *F. fusca*, 43, 57, 71, or 85; 48, 62, 75, or 90; 42, 56, 70, or 84; and 43, 57, 71, or 85 days post sowing, respectively. Linear and hyperbolic regressions of percentage infected plants per block on days post sowing indicated mature-plant resistance in all trials. All models were significant, but hyperbolic curves better fit the data than linear models. Hyperbolic models were used to calculate the number of days post transplant at which a 50% decrease from the predicted percentage infected at transplant age (42 days post sowing) was expected. This was referred to as days post transplant-50 (DPT_{50}). DPT_{50} occurred within nine days post transplant age for all trials, indicating that early TSWV management in pepper is critical.

Introduction

Tomato spotted wilt virus (family *Bunyaviridae*, genus *Tospovirus*, TSWV) causes an estimated annual crop loss of $1 billion worldwide (Goldbach and Peters 1994). In the southern United States, annual losses can exceed $100 million (Pappu 1997). TSWV infects over 900 plant species in more than 80 plant families (Campbell et al. 2007). It is transmitted by at least seven species of thrips, of which tobacco thrips, *Frankliniella fusca* (Hinds), and western flower thrips, *F. occidentalis* (Pergande), are considered the most important in the southeastern United States (Eckel et al. 1996, Groves et al. 2003, Whitfield et al. 2005). Thrips vectors can transmit TSWV only if it is acquired as a first instar (Linford 1962, Sakimura 1962, van de Wetering et al. 1996). Thrips populations and TSWV inoculum increase in winter annual and perennial host plants during the early spring. TSWV is transmitted to crops from summer annual and perennial host plants in the late spring as adult thrips disperse from senescing winter annual host plants (Eckel et al. 1996, Groves et al. 2003, Kahn et al. 2005).

Many factors affect insect-borne virus transmission to a plant including temperature, virus isolate, cultivar, inoculum pressure, and plant age (Populer 1978, Stumpf and Kennedy 2005, 2007). The phenomenon of decreasing susceptibility of a plant to a pathogen as age increases is known as mature-plant resistance (Beemster 1958a, 1958b, 1961). Mature-plant resistance has been observed in various insect-borne plant disease systems including TSWV in tobacco (*Nicotiana tabacum* L.) (Mandal et al. 2007) and peanut (*Arachis hypogaea* L.) (Mandal et al. 2001), aphid transmitted potato leaf roll virus in potato (*Solanum tuberosum*

L.) (Davidson and Sanford 1954, DiFonzo et al. 1994, Knutson and Bishop 1964), and aphid transmitted cucumber mosaic virus in pepper (*Capsicum annuum* L.) (Agrios et al. 1985, Garcia-Ruiz and Murphy 2001). Change in susceptibility to a pathogen can be explained by age rather than transplant shock. Mature-plant resistance commonly is observed in pathogen-plant age relationship experiments in which inoculation was staggered over time but transplanting was performed at the same time for all treatments (Agrios et al. 1985, DiFonzo et al. 1994, Mandal et al. 2007). Of the experiments addressing mature-plant resistance in relation to TSWV, only Mandal et al. (2007) performed a regression of plant infection percentage on plant age, and this was in tobacco. Soler et al. (1998) did not observe mature-plant resistance in a TSWV-susceptible *C. annuum* cultivar across two age classes but observed mature-plant resistance to TSWV across two age classes of a resistant cultivar of *C. chinense* Jacquin. Lack of observed mature-plant resistance in *C. annuum* may be due to several factors including cultivar, isolate, use of mechanical inoculation, and use of two- and four-leaf stage plants, which resulted in all of the plants of both age groups becoming infected. In this paper, we further explore mature-plant resistance in *C. annuum* to thrips-inoculated TSWV using linear and hyperbolic regression analysis on three cultivars of pepper.

Materials and Methods

Two greenhouse (Spring and Fall 2003) and one field trial (Summer 2003) using *C. annuum* cultivar ‘Camelot’ (bell pepper) and one greenhouse trial each (Fall 2003) of the *C. annuum* cultivars ‘Pageant’ and ‘Bounty’ (banana peppers) were carried out in Raleigh, NC

to test the relationship between TSWV prevalence and plant age. For each trial, seeds were germinated on three (field trial) or four (greenhouse trials) calendar dates 14 days apart in a TSWV-free greenhouse. Seedlings were transplanted 35 and 42 days post sowing in field and greenhouse trials, respectively. Seedlings were transplanted into the field or into 30.5 cm diameter pots in a greenhouse and fertilized with 13 g of 14-14-14 granular fertilizer per plant.

The *F. fusca* colony originated from thrips collected in 1995 from peanut (*A. hypogaea*) at the Peanut Belt Research Station in Lewiston, NC, and was maintained on *Phaseolus vulgaris* L. bean pods at 24ºC and 55% relative humidity and a photoperiod of 14:10 (L:D) h. A single isolate of TSWV (TSWV-RG2) was recovered from burley tobacco (*N. tabacum* cultivar 'B21') in 1995 in Carteret County, NC. It was maintained in *Emilia sonchifolia* (L.) via *F. fusca* transmission.

Potentially viruliferous *F. fusca* were obtained by placing first instars from a laboratory colony on excised *E. sonchifolia* leaves infected with TSWV-RG2. After a 48 hour TSWV acquisition period, *F. fusca* were transferred to *P. vulgaris* bean pods in 474 ml plastic cups (Sweetheart Cup Co., Inc., Chicago, IL) with Bedbug 110 mesh (183 x 183 µm openings, 52% open) (Greenthumb Group, Downer's Grove, IL) screened lids and reared to adults. Potentially viruliferous adult *F. fusca* were collected in groups of five (3 female, 2 male unless otherwise specified) into 1.5 ml microcentrifuge tubes (Fisher Scientific, Rochester, NY) 1-2 days after eclosion for pepper plant inoculation. Each plant was caged 1-

2 days after the youngest age class of peppers was transplanted, and one tube of potentially viruliferous *F. fusca* was attached to each plant within the cage using a twist-tie.

Field trial. Three age classes were established by planting seeds 14 days apart, and 12-20 plants per age class were transplanted into the field 35 days post sowing (13 August, 27 August, and 10 September 2003) in a randomized complete block design containing three blocks. No plants were inflorescent at the beginning of the experiment. Variation in plant number was due to plant death caused by deer and crickets.

A flexible, cylindrical cage 20 cm in diameter and 40 cm long comprised of an Agribon+ AG-19 floating row cover (PGI Nonwovens, Inc., Ponchatoula, LA) was placed over the entire plant for those in the youngest age class or over an entire branch including developing leaves that were not yet fully expanded for plants in older age classes. All plants were caged on 12 September 2003, which was two days post transplant for the youngest age class. The cage was secured by gathering and twisting the fabric and fastening a twist-tie at the bottom and top of each cage. No TSWV-infected plants were observed in the field by visual inspection prior the start of the experiment. *F. fusca* were released 37, 51, and 65 days post sowing, and the cages were sealed. Cages were removed four days after *F. fusca* release to avoid weakening the branch on which the cage was secured. Potentially infectious thrips were not killed at the time of cage removal in the Camelot bell pepper field trial. Because the same number of *F. fusca* from the same age cohort reared on an inoculum source from the same *E. sonchifolia* plants was released simultaneously on each pepper plant, potential inoculation pressure was similar across all ages even after cage removal. Therefore, any

movement and subsequent feeding of *F. fusca* was unlikely to affect the mature-plant resistance relationship.

Greenhouse trials. Trials consisted of four age classes planted 14 days apart arranged in a randomized complete block design. Two trials using bell pepper cultivar 'Camelot' and one trial each of cultivars 'Bounty' and 'Pageant' banana pepper were performed. For all trials, only the two oldest age classes were inflorescent at the beginning of each experiment. In the Spring Camelot trial, four of five blocks contained eight plants and the remainder contained four plants per age class. The Fall Camelot, Bounty, and Pageant trials consisted of five blocks with five plants of each age class except that the second oldest age class in the Camelot bell pepper trial contained only four blocks due to insufficient seed germination. Cages consisted of a clear plastic cylinder (5 mm Vivak plastic: AIN Plastics, Greensboro, NC) 42 cm high and 25.4 cm in diameter covered with Bedbug 110 mesh screening (Greenthumb Group, Downer's Grove, IL), and were inserted 6.4 cm into the soil to prevent *F. fusca* from escaping. Five potentially viruliferous *F. fusca* (3 female, 2 male) per plant were released under each cage, except that only males were released on plants in block five of the Fall Camelot bell pepper trial due to a shortage of females. *F. fusca* were released on the Spring Camelot, Fall Camelot, Bounty, and Pageant pepper plants 43, 57, 71, or 85; 48, 62, 75, or 90; 42, 56, 70, or 84; and 43, 57, 71, or 85 days post sowing, respectively.

TSWV Detection and Analysis. Four weeks after the release of *F. fusca*, TSWV infection was determined by DAS-ELISA on a single fully expanded apical leaf and root

samples from each plant using a commercially available kit (Agdia Inc., Elkhart, IN). By assaying these plant parts, systemic infection was tested. A plant was considered positive if either the foliage or root sample absorbance reading at 405 nm was greater than the average of control plant absorbance plus four standard deviations.

Linear and hyperbolic regressions of percentage infected plants per block on days post sowing were performed using PROC REG and PROC NLIN in SAS Version 9.1 (SAS 2002). The following linear model was used:

$$Y_{pi} = S * DPS + I$$

where Y_{pi} is the percentage of TSWV infected pepper plants, S is the slope of the line, DPS is the number of days post sowing on which pepper plants were exposed to viruliferous *F. fusca*, and I is the intercept. Although linear relationships offer simple summary equations, they are often applicable only for a restricted range of data in many biological relationships. Hyperbolic models can allow incorporation of more realistic biological phenomena. For example, a hyperbola has been used to describe crop yield loss with increasing weed density because yield loss cannot exceed maximum yield and the change in yield loss with weed density is not constant (Cousens 1985). Here, hyperbolic models described decrease in percentage of TSWV infected pepper plants with increasing plant age. This is a biologically reasonable relationship since the minimum infection percentage of any plant is zero

regardless of increasing age at time of TSWV exposure, creating a natural asymptote. After Cousens (1985), the following hyperbolic model was used:

$$Ypi = \frac{H * DPS}{1 + \frac{H * DPS}{A}}$$

where Y_{pi} is the percentage of TSWV infected pepper plants, *H* affects the hyperbola's slope, *DPS* is the number of days post sowing on which pepper plants were exposed to potentially viruliferous *F. fusca*, and *A* is the horizontal asymptote.

Using the hyperbolic model, the number of days post transplant at which a 50% decrease from the predicted percentage of infected plants at transplant age (42 days post sowing) is expected was calculated and referred to as days post transplant-50 (DPT_{50}).

Results

Field trial. Field trial results indicate mature-plant resistance (Figure 1). Both the linear ($P = 0.0051$) and hyperbolic regressions were significant ($P = 0.0005$), and explained 69.7 and 88.7% of variation observed in the data, respectively. Regression equations are summarized in Table 1. In this trial, DPT_{50} occurred in nine days.

Greenhouse trials. Similar mature-plant resistance trends were observed in the Camelot bell pepper Spring and Fall greenhouse trials (Figure 2A & B). Regression analyses in Spring and Fall Camelot trials showed significant linear ($P = 0.0042$, $P = 0.0138$) and hyperbolic ($P < 0.0001$, $P < 0.0001$) models (Table 1). The hyperbolic models better described the data than linear models for both the Spring (R^2 = 71.8 vs. 37.4%) and Fall (R^2 = 66.9 vs. 30.7%) Camelot trials. DPT_{50} occurred in seven days in both trials. It should be

noted that a hyperbola consists of two disconnected curves with rapidly changing y values as x values approach an asymptote. The two curves are mirror images, and y values on opposite sides of a vertical asymptote are opposite in sign. The vertical asymptote for the Fall Camelot trial is between days 43 and 44. Therefore, the hyperbolic model for the Fall Camelot trial predicts a negative percentage of infected plants at 42 and 43 days and more than 100% infected plants for 44-45 days post transplant age. DPT_{50} was calculated using a predicted 100% infected plants at 42 days post sowing for the Fall Camelot trial.

In Bounty and Pageant banana peppers, both linear ($P = 0.0007$, $P = 0.0114$) and hyperbolic ($P < 0.0001$, $P < 0.0001$) regressions exhibited significant mature-plant resistance (Figure 3A & B; Table 1), but the hyperbolic models better described TSWV infection in both the Bounty ($R^2 = 81.5$ vs. 48.4%) and Pageant ($R^2 = 67.0$ vs. 30.6%) banana pepper trials. DPT_{50} occurred at three and four days in Bounty and Pageant banana peppers, respectively.

Discussion

In all trials, mature-plant resistance was observed and change in susceptibility to TSWV with age was better described by hyperbolic models than linear models. Linear models likely provide more realistic infection predictions for ages less than those tested because hyperbolic equations predict TSWV prevalence at greater than 100%. If younger pepper plants had been included in these trials, it is likely that change in TSWV prevalence would follow a logistic curve (van der Plank 1963). Extrapolation of TSWV prevalence using either the hyperbolic or linear models would assume the same relationship beyond ages

tested and is not recommended. These models illustrated that pepper plant susceptibility rapidly declines with age. Hyperbolic models accounted for 66.9 to 88.7% of variation seen in the data, but linear models explained only 30.6 to 69.7% of variation. In each trial, the hyperbolic model explained 19 to 36% more variation than the linear model. Hyperbolic models are more biologically realistic than linear models because they include an asymptote of minimum expected TSWV infection percentage regardless of plant age. Hyperbolic models also allow for variation in the rate of change in percentage of TSWV incidence with change in age.

Growers typically transplant pepper seedlings into fields approximately 42 days post sowing. Many growers purchase pepper seedlings rather than growing them from seed, so it is relevant to look at changes in predicted susceptibility beginning at transplant age. Using the hyperbolic models, DPT_{50} occurred in seven to nine days in bell peppers and three to four days in banana peppers. This indicates that a critical period exists shortly after transplanting pepper seedlings during which likelihood of TSWV transmission is greatest at a particular inoculum pressure. Although expected TSWV transmission decreased by at least 50% nine days post transplant age at a specific inoculum pressure, one cannot expect to see a 50% reduction in overall TSWV prevalence in a normal field situation. This is because peppers are transplanted in April and early May, and *F. fusca* populations typically increase during April and May. Therefore, the inoculum pressure and TSWV transmission increase over a period of several weeks after peppers are transplanted (Cho et al. 2000, Groves et al. 2001b, Groves et al. 2003, Populer 1978). However, protection of pepper plants in the first few

weeks post transplanting when the plants are most susceptible to infection is expected to reduce TSWV prevalence and may reduce symptom severity as compared to unprotected plants as has been observed in peanut and tobacco (Mandal et al. 2001 and 2007, McPherson 2006). Reduction in symptom severity in pepper plants may or may not increase yield. Moriones et al. (1998) found that symptom severity in tomato decreased with increasing plant age at the time of inoculation with TSWV, but delay in infection did not affect marketable fruit yield in field grown tomatoes. This is because almost any damage or discoloration renders tomato fruit unmarketable. Even though symptom severity was lessened in late-infected tomatoes, fruit exhibited symptoms. In one of two trials, Chaisuekul et al. (2003) found that delay in TSWV infection of tomato plants increased marketable yield. Agrios et al. (1985) found that delayed infection of peppers by cucumber mosaic virus, which causes discoloration of fruit, decreased symptom severity and increased marketable yield. It is unclear if delayed TSWV infection and reduction of symptom severity in pepper plants would affect marketable yield. This may depend on whether the peppers are sold for fresh fruit retail or processing, and whether late infections reduce subsequent fruit set or fruit size.

The timing of field planting in relation to vector movement can affect overall TSWV incidence. It has been observed that in years when spring vector dispersal occurred within the first few weeks after transplanting tobacco, virus incidence was high compared to other years (Kennedy, unpublished data). Also, Riley and Pappu (2004) noted that early thrips dispersal peaks seemed to be associated with increased TSWV prevalence in tomato fields.

Models to predict exact timing of spring thrips dispersal currently are not available, but mulch and imidacloprid may be used to protect the pepper plants from TSWV infection during the period of highest susceptibility to infection. Black and reflective metallic mulches both reduce thrips vectors landing on plants and TSWV prevalence, but reflective metallic mulch is more effective (Greenough et al. 1990, Harpaz 1982, Kring and Schuster 1992, Momol et al. 2004, Reitz et al. 2003, Riley and Pappu 2004, Scott et al. 1989, Terry 1997). Pepper maturation is dependent upon temperature and black mulch speeds up plant maturation due to light absorption increasing soil temperature (Díaz-Pérez and Batal 2002); mature-plant resistance to TSWV in pepper plants in black mulch is expected to progress more quickly than in peppers planted in bare soil or metallic mulches. Consequently, black stripe reflective mulch, which consists of a central black stripe and shoulders of reflective mulch, may be most desirable. Imidacloprid, which has been shown to reduce TSWV prevalence in tobacco, tomato, and pepper (Groves et al. 2001a, McPherson 2006, McPherson et al. 2002, 2005, Melton et al. 2004a, 2004b, 2004c, Momol et al. 2004), also can be used to protect young pepper plants.

References Cited

Agrios, G. N., M. E. Walker, and D. N. Ferro. 1985. Effect of cucumber mosaic virus inoculation at successive weekly intervals on growth and yield of pepper (*Capsicum annuum*) plants. Plant Dis. 69: 52-55.

Beemster, A.B.R. 1958a. Some aspects of mature plant resistance to viruses in the potato, pp. 212-217. *In* F. Quak, J. Dijkstra, A. B. R. Beemster, and J. P. H. van der Want (eds.), Proceedings, Third Conference on Potato Virus Diseases, 24-28 June 1957, Lisse-Wageningen, Netherlands. H. Veenman and Zonen, Wageningen.

Beemster, A. B. R. 1958b. Transport van X-virus in de aardappel (*Solanum tuberosum* L.) bij primaire infectie. Tijdschr. Plantenziekten. 64: 165-262.

Beemster, A.B.R. 1961. Translocation of potato leaf roll virus and potato virus Y in the potato, pp. 60-67. *In* J. Brandes, R. Bartels, J. Völk, and C. Wetter (eds.), Proceedings, Fourth Conference on Potato Virus Diseases, 12-17 September 1960, Brunswick, Germany. H. Veenman and Zonen N. V., Wageningen.

Campbell, L. R., K. L. Robb, and D. E. Ullman. 2007. The complete Tospovirus-host list. http://www.oznet.ksu.edu/tospovirus/hostlist.html.

Chaisuekul, C., D. G. Riley, and H. R. Pappu. 2003. Transmission of tomato spotted wilt virus to tomato plants of different ages. J. Entomol. Science. 38: 127-136.

Cho, K., J. F. Walgenbach, and G. G. Kennedy. 2000. Daily and temporal occurrence of *Frankliniella* spp. (Thysanoptera: Thripidae) on tomato. Appl. Entomol. Zool. 35(2): 207-214.

Cousens, R. 1985. A simple model relating yield loss to weed density. Ann. Appl. Biol. 107: 239-252.

Davidson, T. R. and G. B. Sanford. 1954. Effect of age of potato foliage on expression of leaf-roll symptoms. Can. J. Botany. 32: 311-317.

Díaz-Pérez, J. C. and K. D. Batal. 2002. Colored plastic film mulches affect tomato growth and yield via changes in root-zone temperature. J. Amer. Soc. Hort. Sci. 127(19): 127-136.

DiFonzo, C. D., D. W. Ragsdale, E. B. Radcliffe, and E. E. Banttari. 1994. Susceptibility to potato leafroll virus in potato: Effects of cultivar, plant age at inoculation, and inoculation pressure on tuber infection. Plant Dis. 78: 1173-1177.

Eckel, C. S., K. Cho, J. F. Walgenbach, G. G. Kennedy, and J. W. Moyer. 1996. Variation in thrips species composition in field crops and implications for tomato spotted wilt epidemiology in North Carolina. Entomol. Exp. Appl. 78: 19-29.

Garcia-Ruiz, H. and J. F. Murphy. 2001. Age-related resistance in bell pepper to cucumber mosaic virus. Ann. App. Biol. 139: 307-317.

Goldbach, R. and D. Peters. 1994. Possible causes of the emergence of tospovirus diseases. Virology. 5: 113-120.

Greenough, D. R., L. L. Black, and W. P. Bond. 1990. Aluminum-surfaced mulch: An approach to the control of tomato spotted wilt virus in solanaceous crops. Plant Dis. 74: 805-808.

Groves, R. L., C. E. Sorenson, J. F. Walgenbach, and G. G. Kennedy. 2001a. Effects of imidacloprid on transmission of tomato spotted wilt tospovirus to pepper, tomato and tobacco by *Frankliniella fusca* Hinds (Thysanoptera: Thripidae). Crop Prot. 20: 439-445.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2001b. Overwintering of *Frankliniella fusca* (Thysanoptera: Thripidae) on winter annual weeds infected with tomato spotted wilt virus and patterns of virus movement between susceptible weed hosts. Phytopathology. 91: 891-899.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2003. Seasonal dispersal patterns of *Frankliniella fusca* (Thysanoptera: Thripidae) and tomato spotted wilt virus occurrence in central and eastern North Carolina. J. Econ. Entomol. 96(1): 1-11.

Harpaz, I. 1982. Nonpesticidal control of vector-borne viruses, pp. 1-21. *In* K.F. Harris and K. Maramorosch (eds.), Pathogens, vectors, and plant diseases: approaches to control. Academic Press, New York.

Kahn, N. D., J. F. Walgenbach, and G. G. Kennedy. 2005. Summer weeds as hosts for *Frankliniella occidentalis* and *Frankliniella fusca* (Thysanoptera: Thripidae) and as reservoirs for tomato spotted wilt tospovirus in North Carolina. J. Econ. Entomol. 98(6): 1810-1815.

Knutson, K. W. and G. W. Bishop. 1964. Potato leafroll virus: effect of date of inoculation on percent infection and symptom expression. Am. Potato J. 38: 227-238.

Kring, J. B., and D. J. Schuster. 1992. Management of insects on pepper and tomato with UV reflective mulches. Florida Entomol. 75(1): 119-129.

Linford, M. B. 1962. Transmission of the pineapple yellow-spot virus by *Thrips tabaci*, pp. 301-324. *In* K. Maramorosch (ed.) Biological transmission of disease agents: symposium held under the auspices of the Entomological Society of America: Atlantic City, 1960. Academic Press, New York.

Mandal, B., H. R. Pappu, and A. K. Culbreath. 2001. Factors affecting mechanical transmission of tomato spotted wilt virus to peanut (*Arachis hypogaea*). Plant Dis. 85: 1259-1263.

Mandal, B., M. L. Wells, N. Martinez-Ochoa, A. S. Csinos, and H. R. Pappu. 2007. Symptom development and distribution of tomato spotted wilt virus in flue-cured tobacco. Ann. Appl. Biol. 151: 67-75.

McPherson, R. M. 2006. Incidence of thrips and tomato spotted wilt tospovirus in flue-cured tobacco protected from early season insect pest infestations. J. Econ. Entomol. 99(3): 764-770.

McPherson, R. M., D. C. Jones, P. F. Bertrand, and A. S. Csinos. 2002. Impact of thrips (Thysanoptera: Thripidae) management practices on suppression of tomato spotted wilt virus and aphid (Homoptera: Aphididae) control in flue-cured tobacco. J. Entomol. Sci. 37(2): 143-153.

McPherson, R. M., M. G. Stephenson, S. S. Lahue, and S. W. Mullis. 2005. Impact of early-season thrips management on reducing the risks of spotted wilt virus and suppressing aphid populations in flue-cured tobacco. J. Econ. Entomol. 98(1): 129-134.

Melton, T. A., C. Fountain, W. Gutierrez, A. Broadwell, and J. Wilson. 2004a. Chemical control of tomato spotted wilt in flue-cured tobacco, p. 38. *In* Flue-cured tobacco disease report. North Carolina Cooperate Extension Service, North Carolina State University: Raleigh, NC.

Melton, T. A., M. Rinehardt, W. Gutierrez, A. Broadwell, and J. Wilson. 2004b. Control of tomato spotted wilt in flue-cured tobacco, p. 34-35. *In* Flue-cured tobacco disease report. North Carolina Cooperate Extension Service, North Carolina State University: Raleigh, NC.

Melton, T. A., B. Spivey, W. Gutierrez, A. Broadwell, and J. Wilson. 2004c. Control of tomato spotted wilt in flue-cured tobacco, p. 33 and 37. *In* Flue-cured tobacco disease report. North Carolina Cooperate Extension Service, North Carolina State University: Raleigh, NC.

Momol, M. T., S. M. Olson, J. E. Funderburk, J. Stavisky, and J. J. Marois. 2004. Integrated management of tomato spotted wilt on field-grown tomatoes. Plant Dis. 88: 882-890.

Moriones, E., J. Aramburu, J. Riudavets, J. Arnó, and A. Laviña. 1998. Effect of plant age at time of infection by tomato spotted wilt tospovirus on the yield of field-grown tomato. Eur. J. Plant Pathol. 104: 295-300.

Pappu, H. R. 1997. Managing tospoviruses through biotechnology: Progress and prospects. Biotechnology and Development Monitor. 32: 1417-1421.

Populer, C. 1978. Changes in host susceptibility with time, pp. 239-262. *In* J.G. Horsfall and E.B. Cowling (eds.) Plant disease: an advanced treatise, vol. 2: how disease develops in populations. Academic Press, New York.

Reitz, S. R., E. L. Yearby, J. E. Funderburk, J. Stavisky, M. T. Momol, and S. M. Olson. 2003. Integrated management tactics for *Frankliniella* thrips (Thysanoptera: Thripidae) in field-grown pepper. J. Econ. Entomol. 96(4): 1201-1214.

Riley, D. G. and H. R. Pappu. 2004. Tactics for management of thrips (Thysanoptera: Thripidae) and tomato spotted wilt virus in tomato. J. Econ. Entomol. 97(5): 1648-1658.

Sakimura, K. 1962. The present status of thrips-borne viruses, pp. 33-40. *In* K. Maramorosch (ed.) Biological transmission of disease agents: symposium held under the auspices of the Entomological Society of America: Atlantic City, 1960. Academic Press, New York.

SAS 2002. SAS/STAT Software, Version 9.1. SAS Institute Inc., Cary, NC.

Scott, S. J., P. J. McLeod, F. W. Montgomery, and C. A. Hander. 1989. Influence of reflective mulch on incidence of thrips (Thysanoptera: Thripidae: Phlaeothripidae) in staked tomatoes. J. Entomol. Sci. 24(4): 422-427.

Soler, S., M. J. Díez, and F. Nuez. 1998. Effect of temperature regime and growth stage interaction on pattern of virus presence in TSWV-resistant accessions of *Capsicum chinense*. Plant Dis. 82: 1199-1204.

Stumpf, C. F. and G. G. Kennedy. 2005. Effects of tomato spotted wilt virus (TSWV) isolates, host plants, and temperature on survival, size and development time of *Frankliniella fusca*. Entomol. Expt. Appl. 114: 215-225.

Stumpf, C. F. and G. G. Kennedy. 2007. Effects of tomato spotted wilt virus isolates, host plants, and temperature on survival, size and development time of *Frankliniella occidentalis*. Entomol. Expt. Appl. 123: 139-147.

Terry, L. I. 1997. Host selection, communication and reproductive behavior, pp. 65-118. *In* T. Lewis (ed.) Thrips as crop pests. CAB International, New York.

van de Wetering, F., R. Goldbach, and D. Peters. 1996. Tomato spotted wilt tospovirus ingestion by first instar larvae of *Frankliniella occidentalis* is a prerequisite for transmission. Phytopathol. 86(9): 900-905.

van der Plank, J. E. 1963. The quantitative effect of horizontal resistance. pp. 249-259. *In* Plant diseases: epidemics and control. Academic Press, New York.

Whitfield, A. E., D. E. Ullman, and T. L. German. 2005. Tospovirus-thrips interactions. Ann. Rev. Phytopathol. 43: 459-489.

Table 1. Estimated values of parameters for linear and hyperbolic fitted curves.

Standard errors follow parameter estimates in parentheses.

	Linear Model			
	S	**I**	***P*-value ($df_{num,den}$)**	**DPT_{50}**
Field Trial				
Camelot	-0.60 (0.15)	36.92 (7.83)	0.005 (1, 7)	--
Greenhouse Trials				
Spring Camelot	-0.96 (0.29)	86.71 (19.38)	0.004 (1, 18)	--
Fall Camelot	-1.00 (0.37)	94.10 (25.74)	0.014 (1, 17)	--
Bounty	-1.60 (0.39)	128.80 (25.28)	0.001 (1, 18)	--
Pageant	-1.09 (0.39)	93.49 (25.40)	0.011 (1, 18)	--

	Hyperbolic Model			
	H	**A**	***P*-value ($df_{num,den}$)**	**DPT_{50}**
Field Trial				
Camelot	-0.01 (0.02)	0.42 (0.59)	0.001 (2, 7)	9
Greenhouse Trials				
Spring Camelot	-0.19 (0.09)	7.07 (2.86)	< 0.001 (2, 18)	7
Fall Camelot	-0.13 (0.08)	5.70 (3.02)	< 0.001 (2, 17)	7
Bounty	-0.11 (0.06)	4.24 (2.26)	< 0.001 (2, 18)	3
Pageant	-0.12 (0.08)	4.92 (2.86)	< 0.001 (2, 18)	4

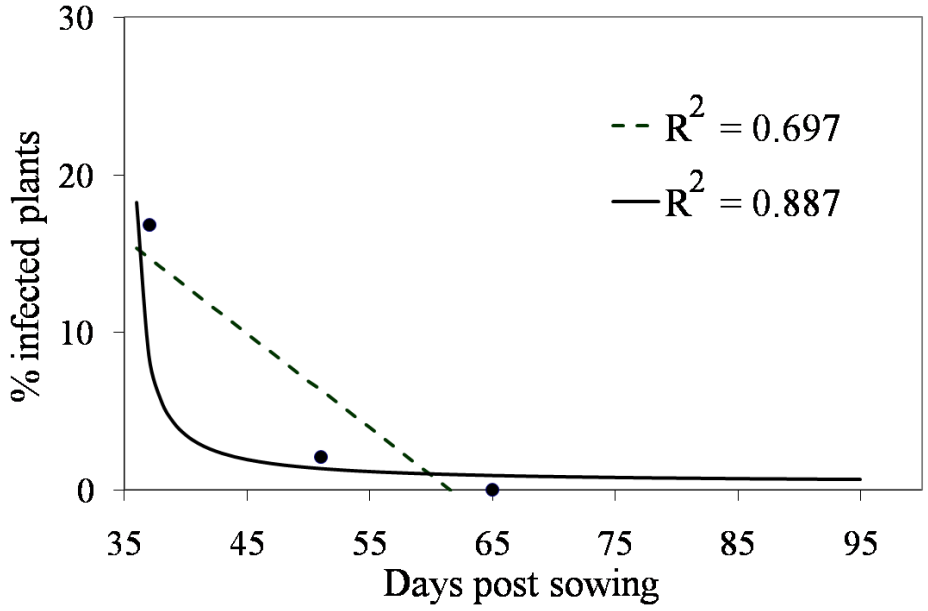


Figure 1. Predicted percentage of TSWV infected Camelot bell pepper plants in a field plot as days post sowing changes. Individual points indicate TSWV prevalence averaged across all blocks.

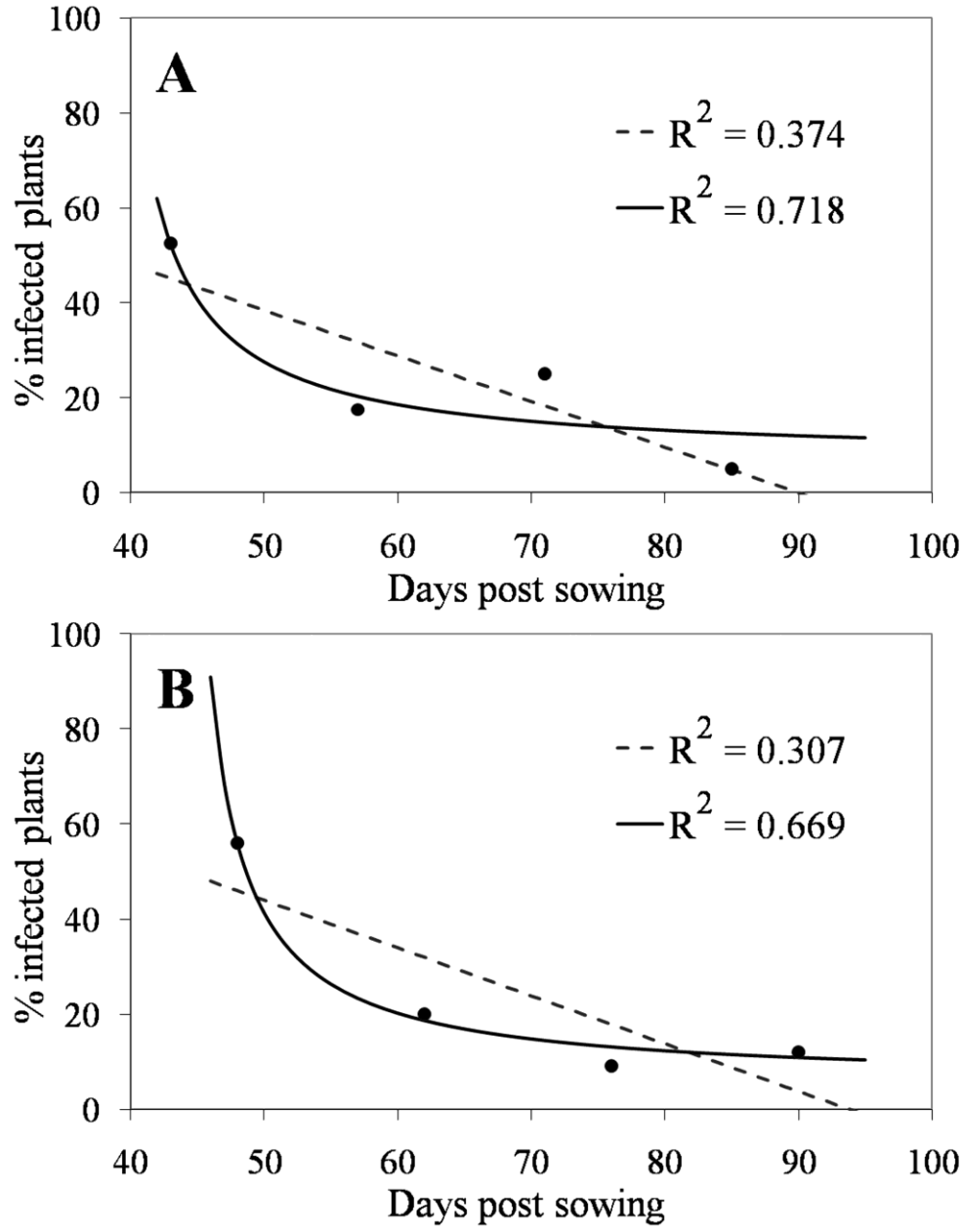


Figure 2. Predicted percentage of TSWV infected Camelot bell pepper plants in Spring (A) and Fall (B) greenhouse trials as days post sowing changes. Individual points indicate TSWV prevalence averaged across all blocks.

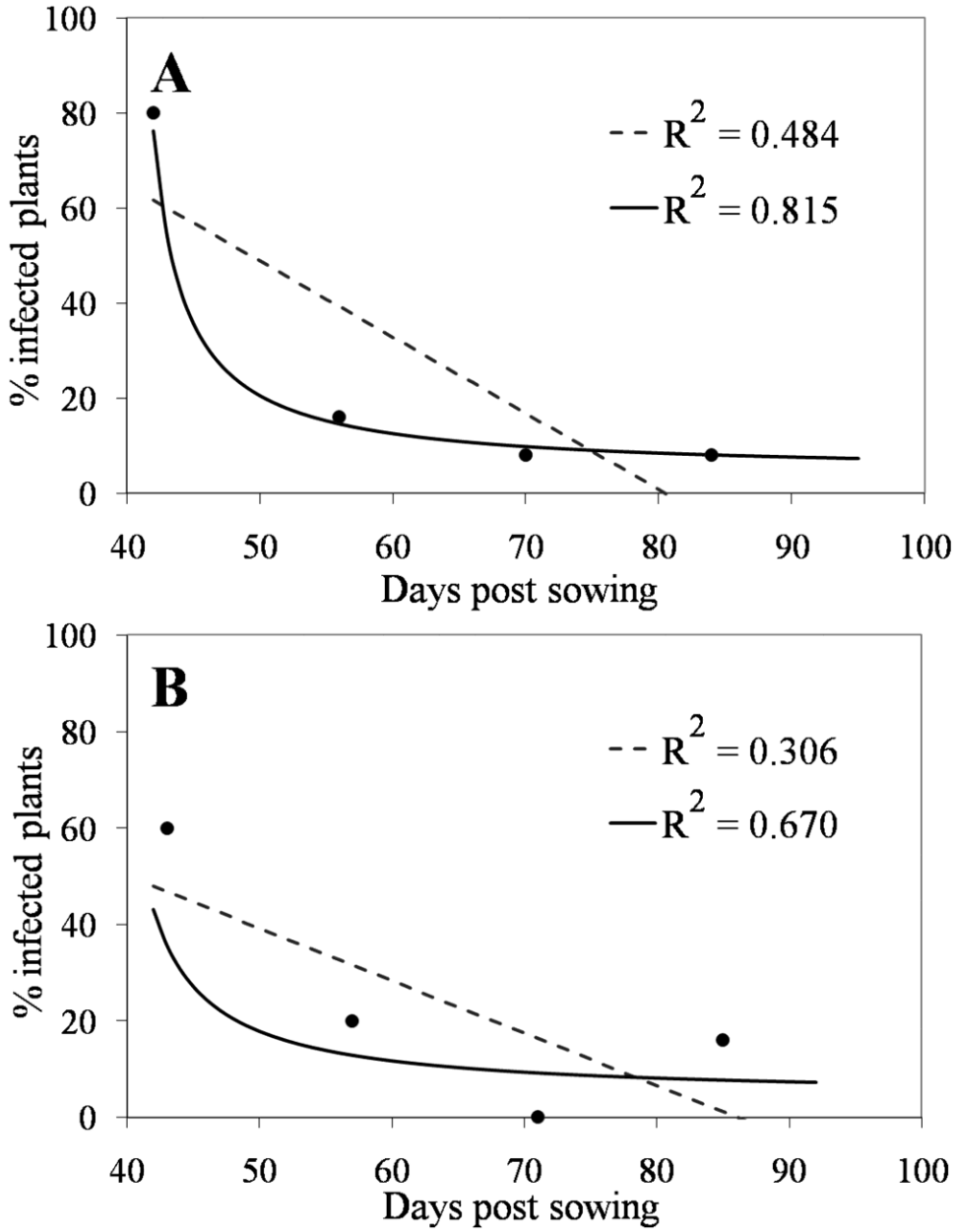


Figure 3. Predicted percentage of TSWV infected Bounty (A) and Pageant (B) banana pepper plants as days post sowing changes. Individual points indicate TSWV prevalence averaged across all blocks.

CHAPTER 2

Management of winter weeds affects *Frankliniella fusca* (Thysanoptera: Thripidae) dispersal

Text as accepted in 2011 for publication in *Environmental Entomology*. Authors: Beaudoin, A. L. P. and G. G. Kennedy.

Abstract

Frankliniella fusca (Hinds) naturally disperses from winter weeds to crops in spring causing direct and indirect damage. Field preparation prior to planting includes use of herbicides or cultivation to kill unwanted vegetation, which adversely affects *F. fusca* host plants and potentially influences *F. fusca* dispersal. Common chickweed, *Stellaria media* (L.), infested with *F. fusca* was used as a model to study effects of timing and type of vegetation management on adult dispersal. Infested weeds were caged and *F. fusca* weekly dispersal was monitored using sticky traps. Weed management treatments performed at an early (14 April – 11 May) or late (two weeks after early treatment) date consisted of glyphosate, paraquat, disking, hoeing, or untreated control. Late glyphosate and hoeing treatments resulted in cumulative dispersal statistically similar to or greater than from control plots. Compared to the control, significantly more *F. fusca* dispersed from the glyphosate and hoeing plots during the three weeks following treatment. More thrips dispersed from the late paraquat treatment one week post application than from the control. Dispersal from the disked treatment and early paraquat treatment was similar to that of the control one to three weeks post treatment. Early treatments resulted in significantly smaller cumulative dispersal than the control in all but one instance. Late disking and paraquat treatments resulted in cumulative *F. fusca* captures that were statistically similar or less than that in the control. Winter weed management type and timing affect *F. fusca* dispersal magnitude and duration.

Introduction

Both landscape-scale factors such as climate and local-scale factors such as host plant characteristics affect thrips population growth and dispersal. General patterns of thrips dispersal can be related to regional temperature and precipitation that influence generation turn-over, flight and mortality (eg. Davidson and Andewartha 1948, Harding 1961, Kirk 1997, Lewis 1997, Lowry 1992, Morsello et al. 2010, Morsello and Kennedy 2009). However, farm-scale variation in thrips populations and adult dispersal also are affected by local factors, which include host plant availability and suitability (Davidson and Andewartha 1948). Land preparation in agricultural fields neighboring recently transplanted susceptible vegetable crops commonly includes disking or, in case of no-till practices often used in soybean, corn and cotton production, use of herbicides such as glyphosate or paraquat to kill unwanted vegetation. Destruction of host plants during land preparation potentially changes natural dispersal patterns of thrips from winter hosts in ways that could result in infestations of young crops in spring.

Tobacco thrips, *Frankliniella fusca* (Hinds), have a broad host range and populations undergo two seasonal dispersals. In fall, *F. fusca* disperse from summer annual and perennial hosts to winter annual and perennial hosts where they overwinter (Chamberlin et al. 1992, Cho et al. 1995, Groves et al. 2001, 2002). Populations of *F. fusca* increase on winter annual hosts in late winter and spring and disperse to summer hosts and crops beginning in spring. In North Carolina, *F. fusca* spring dispersal typically peaks in late May or June (Eckel 1996), and *F. fusca* that feed upon young tomato (*Solanum lycopersicum* L.), pepper (*Capsicum*

annuum L.), tobacco (*Nicotiana tabacum* L.), peanut (*Arachis hypogea* L.) and cotton (*Gossypium spp.* L.) plants, commonly cause early-season damage. This damage is most severe when large infestations occur shortly after transplanting or seedling emergence. Young tomato, pepper, tobacco, and peanut plants can be damaged directly through feeding or indirectly via transmission of *Tomato spotted wilt tospovirus* (TSWV) (Barbour and Brandenburg 1994, Brecke et al. 1996, Cho et al. 1995, Eckel et al. 1996, Gitaitis et al. 1998, Groves et al. 2003, McPherson et al. 1999, Nault et al. 2003).

Because land preparation affects *F. fusca* host quality and is performed during a period of *F. fusca* population growth on winter weeds, we hypothesized that the type and timing of weed management during spring would affect the timing and magnitude of *F. fusca* dispersal, potentially increasing exposure of crops to *F. fusca* when plants are young and most impacted by *F. fusca* damage. Specifically, we hypothesized that killing winter weeds would increase *F. fusca* dispersal for one or more weeks following treatment compared to an untreated control and that a fast-acting herbicide would affect dispersal for a shorter period than a slow-acting herbicide. We further hypothesized that fewer *F. fusca* would disperse when winter weeds were disked than when treated with glyphosate or paraquat, due to partial burial of vegetation resulting from disking. For a given herbicide, we conjectured that early application, when *F. fusca* populations were small, would result in fewer total dispersing *F. fusca* than weed management later in the season when populations were large.

Because common chickweed, *Stellaria media* (L.), is a good reproductive host for thrips and is abundant on North Carolina farms (Groves et al. 2002), it was used as a model

broadleaf winter annual weed in our studies. To test our hypotheses, we subjected small plots of winter weeds to the aforementioned management practices that are commonly used in spring land preparation prior to planting and observed the effects on the timing and magnitude of dispersal of *F. fusca.*

Materials and Methods

Weed Plots and Cages: Chickweed seeds were soaked in a solution of 1:3 chlorine bleach:water for 15 minutes, rinsed three times with water, and allowed to germinate for one week while submerged in 50 ml of water in clear 296 ml plastic drinking cups (Sweethart Cup Company, Owings Mills, MD) before transferring seedlings to soil. For each experiment, each plot consisted of 64 ca. 4 week old (8-10 leaf stage) chickweed plants transplanted in an 8 x 8 plant grid with 10.2 cm between plants within rows and columns. The plants were transplanted into recently disked fields in November 2004, and December 2005 and 2006. Plots were spaced at least 4 m apart and the area between plots was maintained free of vegetation for the duration of each experiment.

All plots were infested with adult *F. fusca* obtained from a laboratory colony originally collected in 1995 from peanut (*A. hypogaea*) at the Peanut Belt Research Station in Lewiston, North Carolina. The colony was maintained on *Phaseolus vulgaris* L. bean pods at 28-30ºC with 50-60% relative humidity and a photoperiod of 14:10 (L:D) h. Adults from the colony were aspirated within three days of eclosion into 146 mm borosilicate glass pasteur pipets (Fisher Scientific, Suwanee, GA) and released on every fourth plant in each plot. For the 2005 and 2006 experiments, five *F. fusca* (4 female, 1 male) were released in late

February and early March, respectively. For the 2007 experiment, ten *F. fusca* (8 female, 2 male) were released in late March to increase the likelihood of observing means separation among treatments. Sufficient *F. fusca* were not available in 2005-2006 to release 10 thrips every 4 plants. Eighty (2005- 2006) or 160 (2007) *F. fusca* were released per plot.

One to two weeks after *F. fusca* were released, each plot was covered by a thrips-proof cage (1.0 m x 1.0 m x 1.0 m) covered with Agribon+ AG-30 floating row cover (PGI Nonwovens, Inc., Ponchatoula, LA) that was anchored to the soil with tie-downs. In late winter, *F. fusca* move short distances from plant to plant but flight is restricted because temperatures are below flight threshold (Groves et al. 2003, Lewis 1997). Therefore populations of *F. fusca* were expected to remain within the weed plots prior to caging. Within each cage, a cylindrical, yellow sticky-trap was suspended 0.70 m above ground level on a bamboo stake in the center of each plot. The trap consisted of PVC pipe (15.2 cm long x 2.54 cm diameter) painted yellow (Krylon Products Group, Cleveland OH) and wrapped with 111 cm^2 of sticky sleeve (Great Lakes IPM, Vestaburg, MI) (Groves et al. 2003). Traps were placed in cages one week prior to any weed treatment and were changed weekly.

Weed Treatments: Weeds were killed at an early or late weed management date ca. two weeks apart using glyphosate, paraquat, disking, or hoeing (Table 1). The hoeing treatment, in which the vegetation desiccates on the soil surface, served as a positive control for detection of increased *F. fusca* dispersal. In the hoeing treatment virtually all of the stem and foliar vegetation remained on the soil surface to desiccate under the cages. Glyphosate (RoundUp Superconcentrate ®, Monsanto Company, Marysville, OH), and paraquat

(Gramoxone Inteon ®, Syngenta, Greensboro, NC) were applied at non-crop label rates (9.4 and 1.1 kg a.i./ha, respectively) using a handheld sprayer with a fan nozzle. Weed plots in the disking treatment were disked twice using a small (less than 3 m) tractor-pulled disk with smooth blades and then recaged. Soil was tilled to a depth of ca. 10 cm, and most weeds were buried by the disking treatment. Desiccation of disked and hoed weeds can occur over several days to more than a week depending on temperature and soil conditions. Weeds in the untreated control plots were allowed to continue to grow and senesce naturally. Disking was performed only on the late treatment date because it was expected that dispersal from disked plots would be less than from late herbicides, potentially making disking a preferable late management option compared to late herbicide application. Time between early and late treatments varied slightly within experiments due to weather constraints. Each experiment was an incomplete block design consisting of the treatments in Table 1. The date of early and late treatments varied year-to-year and location-to-location due to variable climate conditions. The early treatment was applied when the majority of chickweed vegetative growth slowed and plants were producing mature seeds but prior to any visual signs of early senescence. Chickweed typically takes more than a month to senesce after seed production begins. Therefore, treatments were implemented several weeks before senescence of weed hosts to allow time to observe the duration of any treatment effects on *F. fusca* dispersal. This also allowed the maximum time for *F. fusca* population growth, increasing the ability to detect treatment effects, and resulted in treatment dates that varied by year and location. However, using seed production to time treatments did not guarantee that natural senescence

would not overlap treatment effects. Weed senescence began to occur the weeks of 8 June, 2 June, 5 May, and 31 May in the 2005 Oxford, 2006 Oxford, 2006 Kinston, and 2007 Raleigh experiments, respectively. All life stages (egg to adult) of *F. fusca* were present within each cage when treatments were performed, and chickweed plants were mature and actively producing seeds.

Four repetitions of four treatments in a randomized design were included in the 2005 Oxford, North Carolina experiment (Table 1). The early and late treatments were performed on 11 May and 26 May 2005. The 2006 Oxford and Kinston experiments consisted of four randomized blocks each with one repetition of five treatments (Table 1), with early and late weed control performed 21 April and 4 May at Oxford, and 14 April and 1 May at Kinston. The 2007 experiment, conducted in Raleigh, included five randomized blocks each including one repetition of five treatments (Table 1); early and late treatments were applied on 3 May and 17 May 2007. Weed management performed during this date range is consistent with standard farming practices.

Trap Processing and Analysis: When 25 or fewer thrips were on a trap, all thrips were identified to species. When the number of thrips exceeded 25, a subsample of 25 randomly selected thrips were identified to species and the proportion of *F. fusca* was multiplied by the total thrips count to estimate the number of *F. fusca* captured per trap. Thrips to be identified were removed from the trap, mounted on a microscope slide, and identified to species using a key to adult thrips of the Terebrantia suborder (Palmer et al. 1992). Voucher specimens are held at the North Carolina State University Museum. Total *F.*

fusca captured for each treatment was summed from one week after the early treatment application through the remainder of the experiment and was subjected to ANOVA (PROC GLM) and Tukey's mean separation test (alpha = 0.05) (SAS Institute 2005). To analyze treatment differences over time, the number of *F. fusca* was divided by the number of days a trap was under the cage to account for any delay in trap replacement caused by weather restrictions, and average daily *F. fusca* captures were subject to repeated measures ANOVA (PROC GLM) and Tukey's mean separation test (alpha = 0.05) (SAS Institute 2005). An unstructured covariance matrix was found to best fit the data for repeated measures analysis. Additionally, the between-plot effects of early vs. late treatments were tested for significance using contrasts.

Results

Cumulative dispersal. Weed treatment had a significant effect on total *F. fusca* captured (Tables 2, 3). Similar or significantly fewer total *F. fusca* were captured from early glyphosate, and significantly fewer total *F. fusca* were captured from early paraquat and early hoeing plots than from control plots (Table 3).

Like early glyphosate treatment effects, total *F. fusca* from late disking plots was similar or significantly less than from control plots (Table 3). The late paraquat treatment resulted in fewer total *F. fusca* captured compared to the control (Tables 2, 3). However, similar or significantly more total *F. fusca* were captured from late glyphosate and late hoeing treatments than from the control (Table 3).

All early vs. late treatment contrast comparisons were significant, indicating that more *F. fusca* were captured from plots treated at a late date than at an early date (Table 4). For the Raleigh 2007 trial, an additional contrast comparing the early herbicide treatment (paraquat) and the late herbicide treatments (paraquat and glyphosate) was tested and found to be significant (Table 4). More *F. fusca* were captured from late herbicide plots than the early paraquat plot.

Weekly dispersal. Weed treatment also significantly affected the average magnitude of *F. fusca* captured through time (Table 2, Figure 1). Dispersal, as indicated by number of thrips caught on traps, was low for all treatment and control plots prior to the late treatment application dates regardless of treatment and whether plots were initially infested with 80 *F. fusca* (2005-2006 means ≤ 1.41/day) or 160 *F. fusca* (2007 means ≤ 5.34/day; Figure 1a-d). In two of three experiments containing the early glyphosate treatment, average daily *F. fusca* captured from the early glyphosate plots were similar to the control plots for three weeks post application (Figure 1a & c). However, in a third experiment, significantly more average daily *F. fusca* were captured from the early glyphosate plots compared to the control plots one week following the glyphosate application; numbers of *F. fusca* subsequently declined and remained low (Figure 1b). More *F. fusca* were captured from early hoeing plots than the control one week after treatment, but captures were similar the following two weeks and persisted at low levels for the duration of the experiment (Figure 1a). In contrast, the average daily number of *F. fusca* captured from the early paraquat treatment was never significantly

greater than the control, and the magnitude of dispersal remained low for the rest of the experiment like other early treatments (Figure 1d).

For all late herbicide treatments, an increase in average daily *F. fusca* dispersal compared to the control was observed in one or more experiments (Figure 1). In contrast to the early glyphosate treatment that caused a significant increase in average daily *F. fusca* captured for one week compared to the control (Figure 1b), late glyphosate treatment effects lasted two weeks longer in two of four trials (Figure 1b & c). In the other two trials, dispersal increased from the late glyphosate plots two weeks after application before declining steeply, but the rate of increase was less than of control plots, from which the number of dispersing thrips increased dramatically as weeds naturally senesced (Figure 1a & d). Plots receiving a late paraquat application showed a significant increase in average daily *F. fusca* dispersal for one week compared to the control (Figure 1d).

Dispersal effects for non-herbicide plots varied by weed pressure on the soil surface post treatment. The magnitude of average daily dispersal of *F. fusca* was significantly increased for three weeks post hoeing compared to the control (Figure 1 b & c), during which time weeds slowly desiccated under cages on the soil surface. The late disking treatment, which almost completely buried weeds, did not increase average daily *F. fusca* dispersal compared to control plots in any week for any experiment (Figure 1 b-d).

Discussion

Our findings support the hypothesis that vegetation management in late spring changes the quality of *F. fusca* host plants and influences the timing and magnitude of *F.*

fusca dispersal from winter weeds. They also support our hypothesis that killing winter weeds increases *F. fusca* dispersal magnitude compared to an untreated control for one or more weeks depending on the timing and type of weed management. Overall, an increase in numbers of dispersing *F. fusca* relative to untreated weeds was observed for all treatments in one or more trials except for the late disking and early paraquat treatments; however, effects of treatments on the magnitude and duration of increased dispersal were not always consistent across all experiments.

Early weed management, applied when thrips populations were low, either did not result in increased dispersal of *F. fusca*, as measured by trap catches, or caused an increase that lasted for a period of only one week. Early treatment timing was based on when the plants matured and actively produced seeds. Because of climatic variation from year to year and location to location, it is probable that tobacco thrips populations varied in size from trial to trial when treatments were applied. This could explain why the duration and magnitude of treatment effects varied by trial. However, our results show that for each trial, significantly fewer *F. fusca* were captured from early treatments compared to late treatments (Table 4). The early glyphosate treatment caused a 1-week increase in dispersal in only one of three trials in which it was included (Figure 1b), and early hoeing caused a similar 1-week increase in the only trial in which it was included (Fig 1a). In both cases, the increases were small. The early paraquat treatment did not increase the number of dispersing *F. fusca* captured in the only trial in which it was included (Figure 1d). Failure to consistently observe increases in *F. fusca* dispersal following early weed management likely reflects the small numbers of

thrips present at the time the early treatments were applied. In all cases, the total numbers of *F. fusca* dispersing from weeds later in the season were greatly reduced by the early management of winter weeds relative to the control and late applied weed management treatments with the exception of late disking, which partially buried the weeds.

Effects of late vegetation management on number and duration of *F. fusca* dispersal relative to the control, in which the vegetation was allowed to senesce naturally, were more variable among treatments than early management. In three of four experiments, the late glyphosate application significantly increased the numbers of *F. fusca* dispersing relative to the control for periods of up to three weeks following application. The only exception was in the 2007 trial when natural senescence of plants in the control coincided with, but progressed more slowly than senescence in the glyphosate treated plots (Figure 1d). In this case, the number of dispersing *F. fusca* from the glyphosate treatment increased considerably during the two weeks following application and was significantly greater than the control during the first week; however, dispersal from the control during the second week increased much more rapidly and reached higher numbers than from the glyphosate treatment. Multiple-week increases in numbers of dispersing *F. fusca* from late glyphosate treated plots may be explained by gradual adult *F. fusca* dispersal from plants that died over a period of ca. 10 days, which spanned two trapping periods. Increased dispersal observed during the third week following late applications of glyphosate likely reflects dispersal of adults from immature thrips that were able to complete larval development on the senescing plants and pupate before glyphosate treated plants died.

Number of dispersing *F. fusca* also increased from late paraquat plots relative to the control, but the effect lasted for only one week, likely reflecting dispersal of adults from the dying plants and from pupae produced before the plants died. By two weeks post-application, the numbers of dispersing thrips in late paraquat treatment were statistically similar to the late disking treatment, which did not cause an observed increase in number of dispersing *F. fusca*. Overall, our weekly results suggest that late weed management with herbicides causes a longer period of increased numbers of dispersing *F. fusca* than early management.

Concordant with our expectations, the maximum observed duration of the increased dispersal effect of slower-acting glyphosate was longer than for faster-acting paraquat (late glyphosate increased *F. fusca* dispersal three weeks post treatment in the Oxford 2006 trial but late paraquat increased dispersal for only one week in the Raleigh 2007 trial). However, because paraquat was tested in only one trial, it is possible that paraquat application could increase *F. fusca* dispersal for multiple weeks under different weather conditions. The shorter period of increased dispersal from paraquat plots compared to glyphosate plots could also be due to a direct suppressive effect of paraquat on the tobacco thrips population, which would have reduced the number of thrips available to disperse (Beaudoin and Kennedy, unpublished). Mortality due to paraquat exposure has been documented in several species of arthropods, including *Drosophila melanogaster* Meigen (Drosophilidae), the parasitoid *Eretmocerus debachi* Rose & Rosen (Aphelinidae), and the predatory mite, *Neoseiulus fallacis* (Garman) (Phytoseiidae) (Hosamani and Muralidhara 2010, Metzger and Pfeiffer 2002, Uygun *et al*. 1994).

As anticipated, fewer *F. fusca* dispersed after disking of winter weeds than late applications of glyphosate or paraquat. Disking almost completely buried most of the foliage and likely prevented any increase in dispersal. In contrast, late hoeing left virtually all of the weed foliage on the soil surface and resulted in an increase in *F. fusca* dispersal relative to the control that lasted as long as three weeks. Although hoeing is not a viable weed management strategy for commercial growers, the dissimilar effects of late hoeing and disking on thrips dispersal are consistent with the hypothesis that the magnitude and duration of increased dispersal following a weed management depends on the rate at which the suitability of treated plants for thrips feeding and development declines following treatment.

For a given herbicide, we conjectured that use of an early weed management when *F. fusca* populations were small would result in fewer total dispersing *F. fusca* than weed management later in the season when populations were high. Glyphosate effects on dispersal are consistent with this hypothesis. However, similar totals of *F. fusca* were captured from early and late paraquat treatments. If paraquat had a direct suppressive effect on *F. fusca* populations, it is possible that only small numbers of *F. fusca* survived paraquat treatments.

The timing of *F. fusca* dispersal affects the potential for damage to crops because young plants are most susceptible to direct and indirect *F. fusca* damage. Many crops become less susceptible to *F. fusca* feeding damage and tomato spotted wilt as they mature (Beaudoin et al. 2009, Mandal et al. 2001, 2007, Breke et al. 1996, Mississippi State University Extension 2010). Overall, our results indicate that late weed management with herbicides causes a longer period of elevated dispersal by *F. fusca* than early management. Because

vegetation management is performed in April and May when *F. fusca* populations are increasing, it is prudent to choose tactics that do not promote *F. fusca* dispersal that might lead to elevated infestations in nearby crops. Based on our results, the most conservative approach to minimizing *F. fusca* dispersal to susceptible crops when using glyphosate to kill weeds in nearby fields is to apply it at least four weeks prior to seedling emergence or transplanting of the susceptible crop. Paraquat should be applied at least two weeks prior to transplant or seedling emergence. Vegetation can be disked at any time without increasing *F. fusca* dispersal compared to no vegetation management. In cases where disking vegetation is not practical and young, susceptible crops will be growing near a weedy area in less than two weeks, using no vegetation management may be the best option to avoid increased *F. fusca* dispersal when the plants are most susceptible to injury and infection.

References Cited

Barbour, J. D and R. L. Brandenburg. 1994. Vernal infusion of thrips into North Carolina peanut fields. J. Econ. Entomol. 87: 446-451.

Beaudoin, A. L. P., N. D. Kahn, and G. G. Kennedy. 2009. Bell and banana pepper exhibit mature-plant resistance to tomato spotted wilt tospovirus transmitted by *Frankliniella fusca* (Thripidae: Thysanoptera). J. Econ. Entomol. 102: 30-35.

Breke, B. J., J. E. Funderburk, I. D. Teare, and D. W. Gorbet. 1996. Interaction of early-season herbicide injury, tobacco thrips injury, and cultivar on peanut. Agron. J. 88: 14-18.

Chamberlin, J. R., J. W. Todd, R. J. Beshear, A. K. Culbreath, and J. W. Demski. 1992. Overwintering hosts and wingform of thrips, *Frankliniella* spp., in Georgia (Thysanoptera: Thripidae): implications for management of spotted wilt disease. Environ. Entomol. 21: 121-128.

Cho, K. C., S. Eckel, J. F. Walgenbach, and G. G. Kennedy. 1995. Overwintering of thrips (Thysanoptera: Thripidae) in North Carolina. Environ. Entomol. 24: 58-67.

Davidson, J. and H. G. Andrewartha. 1948. The influence of rainfall, evaporation and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imagines* (Thysanoptera). J. Animal Ecol. 17: 200-222.

Eckel, C. S., K. Cho, J. F. Walgenbach, G. G. Kennedy, and J. W. Moyer. 1996. Variation in thrips species composition in field crops and implications for tomato spotted wilt epidemiology in North Carolina. Entomol. Exp. Appl. 78: 19-29.

Gitaitis, R. D., C. C. Dowler, and R. B. Chalfant. 1998. Epidemiology of tomato spotted wilt in pepper and tomato in southern Georgia. Plant Dis. 83: 752-756.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2001. Overwintering of *Frankliniella fusca* (Thysanoptera: Thripidae) on winter annual weeds infested with tomato spotted wilt virus and patterns of virus movement between susceptible hosts. Phytopathol. 91: 891-899.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2002. The role of weed hosts and tobacco thrips, *Frankliniella fusca*, in the epidemiology of tomato spotted wilt virus. Plant Dis. 86: 573-582.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2003. Seasonal dispersal patterns of *Frankliniella fusca* (Thysanoptera: Thripidae) and tomato spotted wilt virus occurrence in central and eastern North Carolina. J. Econ. Entomol. 96: 1-11.

Harding, J. A. 1961. Effect of migration, temperature, and precipitation on thrips infestations in south Texas. J. Econ. Entomol. 54: 77-79.

Hosamani, R. and Muralidhara. 2010. Prophylactic treatment with *Bacopa monnieri* leaf powder mitigates paraquat-induced oxidative perturbations and lethality in *Drosophila melanogaster*. Indian J. Biochem. Biophys. 47: 75-82.

Kirk, W. D. J. 1997. Distribution, abundance and population dynamics, pp. 217-257. *In* T. Lewis (ed.), Thrips as Crop Pests. CABI, Oxon, UK.

Lewis, T. 1997. Flight and dispersal, pp. 175-195. *In* T. Lewis (ed.), Thrips as Crop Pests. CABI, Oxon, UK.

Lowry, V. K., J. W. Smith, and F. L. Mitchell. 1992. Life-fertility tables for *Frankliniella fusca* (Hinds) and *F. occidentalis* (Pergande) (Thysanoptera: Thripidae) on peanut. Ann. Entomol. Soc. Am. 85: 744-754.

Mandal, B., H. R. Pappu, and A. K. Culbreath. 2001. Factors affecting mechanical transmission of tomato spotted wilt virus to peanut (*Arachis hypogaea*). Plant Dis. 85: 1259-1263.

Mandal, B., M. L. Wells, N. Martinez-Ochoa, A. S. Csinos, and H. R. Pappu. 2007. Symptom development and distribution of tomato spotted wilt virus in flue-cured tobacco. Ann. Appl. Biol. 151: 67-75.

McPherson, R. M., H. R. Pappu, and D. C. Jones. 1999. Occurrence of five thrips species on flue-cured tobacco and impact on spotted wilt disease incidence in Georgia. Plant Dis. 83: 765-767.

Metzger, J. A. and D. G. Pfeiffer. 2002. Topical toxicity of pesticides used in Virginia vineyards to the predatory mite, *Neoseiulus fallacis* (Garman). J. Entomol. Sci. 37: 329-337.

Mississippi State University Extension 2010. Publication 2302: Biology and control of thrips on seedling cotton. Mississippi State University Extension Service, pub. http://msucares.com/pubs/publications/ Layton, B. and J. T. Reed.

Morsello, S. C. and G. G. Kennedy. 2009. Spring temperature and precipitation affect tobacco thrips, *Frankliniella fusca*, population growth and tomato spotted wilt virus spread within patches of the winter annual weed *Stellaria media.* Entomol. Exp. Appl. 130: 138-148.

Morsello, S. C., A. L. P. Beaudoin, R. L. Groves, B. A. Nault, and G. G. Kennedy. 2010. The influence of temperature and precipitation on spring dispersal of *Frankliniella fusca* changes as the season progresses. Entomol. Exp.Appl. 134: 260-271.

Nault, B.A., J. Speese III, D. Jolly, and R. L. Groves. 2003. Seasonal patterns of adult thrips dispersal and implications for management in eastern Virginia tomato fields. Crop Prot. 22: 505-512.

Palmer, J. M., L. A. Mound, and G. J. du Haeume. 1992. IIE guides to insects of importance to man, vol. 2. Thysanoptera (ed. by CR Betts), pp. 73. International Institute of Entomology, CAB International, Wallingford, UK.

SAS Institute, Inc. 2005. SAS® 9.1.3 Intelligence Platform: Single-User Installation Guide. Cary, North Carolina, USA.

Uygun, N., C. Sengonca, M. R. Ulusoy, and U. Kersting. 1994. Toxicity of some pesticides to *Eretmocerus debachi* (Hymenoptera, Aphelinidae), an important parasitoid of *Parabemisia myricae* (Homoptera, ,Aleyrodidae). Bull. Entomol. Res. 84: 119-122.

Table 1. Weed management treatments by location and year. Treatments were performed at an early or late date consistent with timing of land preparation in the North Carolina farmscape. Untreated control plots were present in each experiment.

Treatment[1]	2005 Oxford	2006 Oxford	2006 Kinston	2007 Raleigh
Glyphosate	early, late	early, late	early, late	late
Hoeing	early	late	late	--
Disking	--	late	late	late
Paraquat	--	--	--	early, late

Early and late treatments were performed for the indicated experiment as follows: 2005 Oxford, 11 and 26 May; 2006 Oxford, 21 April and 4 May; 2006 Kinston, 14 April and 1 May; and 2007 Raleigh, 3 and 17 May.

Table 2. ANOVA results for overall weed management treatment effect on cumulative *F. fusca* captured and treatment*week interaction effect on average *F. fusca* captured.

	Treatment effect, cumulative *F. fusca*			**Treatment*week interaction, repeated measures**		
Experiment	**F-value**	**d.f.**	**p-value**	**F-value**	**d.f.**	**p-value**
2005 Oxford	13.2	3, 12	0.0004	13.2	15, 60	< 0.0001
2006 Oxford	16.2	4, 12	< 0.0001	20.9	24, 72	< 0.0001
2006 Kinston	44.4	4, 12	< 0.0001	24.4	24, 72	< 0.0001
2007 Raleigh	10.0	4, 16	0.0003	8.9	24, 96	< 0.0001

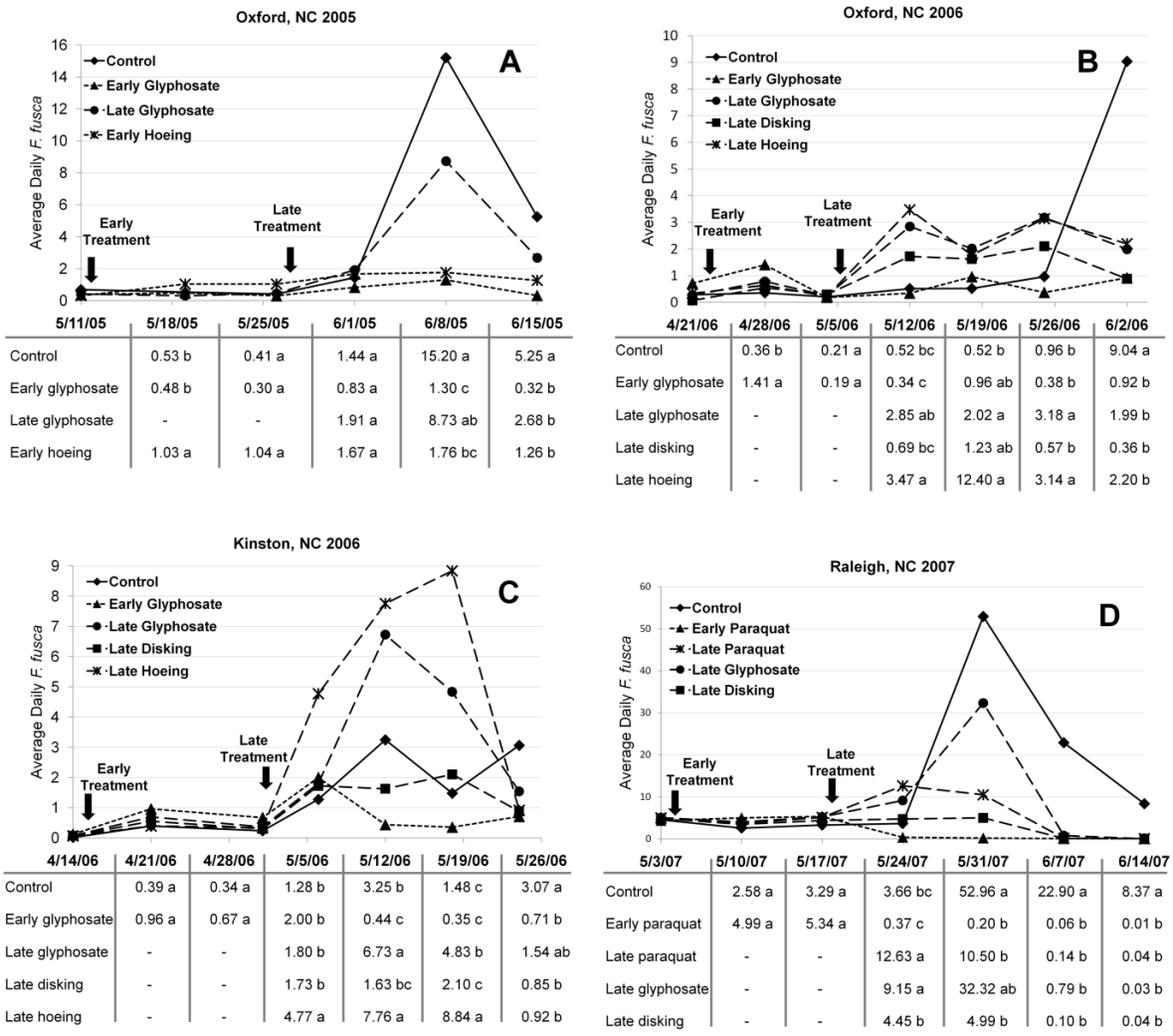
Table 3. Tukey's multiple pairwise comparisons of vegetation treatment for total dispersing *F. fusca* captured on sticky traps from treatment application through the termination of the experiment. Different letters indicate significantly distinct groups of treatments (α = 0.05).

Treatment	Oxford 2005	Oxford 2006	Kinston 2006	Raleigh 2007
Control	153.68 a	80.92 a	67.25 c	1313.50 a
Early glyphosate	22.07 c	28.40 b	35.93 c	--
Early hoeing	45.43 bc	--	--	--
Early paraquat	--	--	--	157.23 b
Late glyphosate	94.32 ab	77.52 a	111.75 b	721.33 ab
Late Hoeing	--	80.15 a	160.91 a	--
Late disking	--	25.33 b	50.15 c	240.82 b
Late paraquat	--	--	--	450.30 b

Table 4. Contrasts for early vs. late between-treatment effects.

Trial	Contrast coefficients[2]	F-value	P-value[1]	df
Oxford 2005	early vs. late treatments **-1** E glyphosate, **-1** E hoeing, **2** L glyphosate	**8.72**	< **0.0001**	5, 54
Oxford 2006	early vs. late treatments **-3** E glyphosate, **1** L glyphosate, **1** L hoeing, **1** L disking	**7.05**	< **0.0001**	6, 72
Kinston 2006	early vs. late treatments **-3** E glyphosate, **1** L glyphosate, **1** L hoeing, **1** L disking	**37.08**	< **0.0001**	6, 72
Raleigh 2007	early vs. late treatments **-3** E paraquat, **1** L paraquat, **1** L glyphosate, **1** L disking	**3.42**	**0.0041**	6, 96
	early herbicide vs. late herbicide treatments **-2** E paraquat, **1** L paraquat, **1** L glyphosate	**5.29**	< **0.0001**	6, 96

[1] $\alpha = 0.05$ for the 2005-2006 trials; The Bonferroni correction for the 2007 trial, and significance was evaluated at $\alpha = 0.025$. [2] E and L stand for early and late treatment applications, respectively.



	5/11/05	5/18/05	5/25/05	6/1/05	6/8/05	6/15/05
Control	0.53 b	0.41 a	1.44 a	15.20 a	5.25 a	
Early glyphosate	0.48 b	0.30 a	0.83 a	1.30 c	0.32 b	
Late glyphosate	-	-	1.91 a	8.73 ab	2.68 b	
Early hoeing	1.03 a	1.04 a	1.67 a	1.76 bc	1.26 b	

	4/21/06	4/28/06	5/5/06	5/12/06	5/19/06	5/26/06	6/2/06
Control	0.36 b	0.21 a	0.52 bc	0.52 b	0.96 b	9.04 a	
Early glyphosate	1.41 a	0.19 a	0.34 c	0.96 ab	0.38 b	0.92 b	
Late glyphosate	-	-	2.85 ab	2.02 a	3.18 a	1.99 b	
Late disking	-	-	0.69 bc	1.23 ab	0.57 b	0.36 b	
Late hoeing	-	-	3.47 a	12.40 a	3.14 a	2.20 b	

	4/14/06	4/21/06	4/28/06	5/5/06	5/12/06	5/19/06	5/26/06
Control	0.39 a	0.34 a	1.28 b	3.25 b	1.48 c	3.07 a	
Early glyphosate	0.96 a	0.67 a	2.00 b	0.44 c	0.35 c	0.71 b	
Late glyphosate	-	-	1.80 b	6.73 a	4.83 b	1.54 ab	
Late disking	-	-	1.73 b	1.63 bc	2.10 c	0.85 b	
Late hoeing	-	-	4.77 a	7.76 a	8.84 a	0.92 b	

	5/3/07	5/10/07	5/17/07	5/24/07	5/31/07	6/7/07	6/14/07
Control	2.58 a	3.29 a	3.66 bc	52.96 a	22.90 a	8.37 a	
Early paraquat	4.99 a	5.34 a	0.37 c	0.20 b	0.06 b	0.01 b	
Late paraquat	-	-	12.63 a	10.50 b	0.14 b	0.04 b	
Late glyphosate	-	-	9.15 a	32.32 ab	0.79 b	0.03 b	
Late disking	-	-	4.45 b	4.99 b	0.10 b	0.04 b	

Figure 1. Average daily dispersing *F. fusca* captured on sticky traps by location and year. Early and late treatments are indicated by short and long dashed lines, respectively. Means and Tukey's mean separation of average daily *F. fusca* captured on aerial traps are indicated below the trap collection date. Different letters indicate significantly distinct groups of treatments ($\alpha = 0.05$).

CHAPTER 3

Spatial patterns of *Frankliniella fusca* (Thysanoptera: Thripidae) captures and *tomato spotted wilt virus* prevalence in relation to weedy field margins

Abstract

For many insects, regional dispersal patterns are affected by weather patterns, but field-scale distribution of insects is affected by whether the insects actively or passively colonize plant hosts. Furthermore, insect distribution may affect the spatial pattern of insect-borne plant pathogens. The tobacco thrips, *Frankliniella fusca* (Hinds), is the primary vector of *tomato spotted wilt virus* for many crops in North Carolina, including tobacco, *Nicotiana tabacum* L. Because *F. fusca* disperse from winter annual and perennial weed hosts to crops and summer annual weeds, we studied whether the relationship between number of *F. fusca* captured on sticky traps is related to distance from natural weed hosts using grids of traps placed within recently disked fields of bare soil during peak *F. fusca* flights. Additionally, tomato spotted wilt (TSW) prevalence was recorded in separate, mature tobacco fields and related to weed proximity. We hypothesized that a greater abundance of *F. fusca* and TSW prevalence would be observed with increasing proximity to natural weed hosts. We performed regression analysis and utilized field-scale and within-field spatial statistics to analyze patterns of *F. fusca* and TSW distribution. Distance to weedy field margins was significantly related to the number of *F. fusca* captured in three of four fields and to TSW prevalence in two of two fields; however, we observed patterns contrary to our hypothesis and found increasing numbers of *F. fusca* on traps and increasing TSW prevalence with increasing distance from weeds. Clustering was observed in all fields and generally reflected relationships observed using regression analysis.

Introduction

Patterns of insect colonization are of special importance to insect-borne disease epidemiology, in which disease spread is dependent upon vector movement. Tospoviruses are transmitted exclusively by several species of thrips, and the importance of a given species in tospovirus transmission depends on both the specific virus and geographic region (Whitfield *et al.* 2005). The tobacco thrips, *Frankliniella fusca* (Hinds), is the primary vector of *tomato spotted wilt virus* (TSWV, Family Bunyaviridae, genus *Tospovirus*) for many crops in North Carolina, including tobacco, *Nicotiana tabacum* L. Regional dispersal patterns of *F. fusca* are driven by climate (Morsello *et al*. 2008, 2010), but field-scale patterns of *F. fusca* colonization are undocumented. *F. fusca* dispersal is seasonal and cyclical; adults begin to disperse from summer annual and perennial hosts in the fall, and populations increase on winter annual weeds in the late winter and early spring, during which time thrips spread TSWV plant-to-plant. Because *F. fusca* is a generalist herbivore and TSWV is known to infect over 800 species of plants across more than 80 plant families, both vector and inoculum source are prevalent throughout the North Carolina farmscape. As winter weed hosts decline, viruliferous *F. fusca* disperse to other hosts, including crops and summer annual weeds (Cho *et al*. 1995, Groves *et al*. 2001, 2002). Peak spring *F. fusca* dispersal in North Carolina typically begins in May and lasts several weeks (Groves *et al*. 2001, 2003, Morsello *et al*. 2008). A more specific understanding of *F. fusca* distribution on a field-scale provides a better understanding of the insect's behavior and may be of practical value for TSW management.

In general, insect colonizers may actively choose where to land, be passively deposited in a location, or arrive at a new location by a mix active and passive movement (Pasek 1988). The type of movement affects distribution patterns within a habitat. Distribution of active colonizers is non-random since the insects choose where to alight, though the exact distribution of active colonizers depends on insects' strategies of selecting hosts. Some herbivorous active colonizers preferentially immigrate to edges of habitat patches due to differences in edge- and interior-plant characteristics. Edge-plants may differ from interior-plants due to reduced competition with plants for space, variation in exposure to sun and shade, and different moisture conditions leading to variation in plant shape, size, nutrient content, and levels of secondary compounds (*e.g*. Crone and Jones 1999, Iason and Hester 1993, Westoby *et al*. 2002). Concentrations of insects at the edges of habitat patches have been related to insects preferentially selecting hosts based on plant quality, microhabitat preference, and frequency of encounter since edges are happened upon more frequently than interiors of patches (Collinge and Louda 1989, Jones 1977). In contrast, some herbivorous insects are known to be concentrated in the interiors of habitat patches. It has been suggested that because host plants are more concentrated in the interior of a patch than around the edges, some insects prefer to occupy areas with a greater concentration of habitat resources (Root 1973). Other colonizers exhibit a direct relationship between insect concentration and proximity to host plants from which they dispersed, creating gradients within a field rather than more localized edge effects. Examples are numerous and span across many insect and

arthropod orders (eg. Grevstad and Herzig 1997, Hanski *et al*. 1994, Wilson and Morton 1993, Stein *et al*. 1994).

Passive colonizers, most commonly dispersed by wind, exhibit a range of distributions, some of which differ from those of active colonizers. Often small, weak flying insects can control whether or not they take flight (dispersal initiation) but cannot control flight paths (Pasek 1988). Turbulent wind can deposit insects randomly across a field or eddies may lead to patchy insect distribution via insect "fall-out" or impaction with plants or other objects (Pasek 1988). In other cases, deposition patterns of insects are affected by windbreaks. Lewis found that both natural (eg. hedgerows, treelines) and artificial (fences) windbreaks caused an accumulation of weak flying insects in a "pocket" of air moving circularly on the lee side of windbreaks while small insects outside of this pocket were carried away from the windbreak (Lewis 1970).

In general, small, weak flying insects, such as thrips, tend to be more passive fliers than larger, strong flying insects. Although thrips can be carried long distances in far-moving air masses, observed gradients of increasing concentration of western flower thrips, *F. occidentalis* (Pergande), with proximity to weed hosts are evidence that at least some thrips are active colonizers on a local scale (Groves *et al*. 2001). Gradients of *tomato spotted wilt virus* prevalence similar to *F. occidentalis* dispersal patterns have been observed in lettuce (Coutts *et al*. 2004).

To better understand dispersal of *F. fusca* at a field-scale, we studied the relationship between number of *F. fusca* captured and distance from natural weed hosts using grids of

aerial sticky traps that were placed within recently disked fields of bare soil during peak *F. fusca* flights. In addition, TSW prevalence was recorded in separate, mature tobacco fields to test for relationships to weed proximity. Because spatial patterns of *F. fusca* abundance affect the potential for TSWV spread and weedy margins serve as sources for both vector and virus, we hypothesized that a greater abundance of *F. fusca* and TSW prevalence would be observed with increasing proximity to natural weed hosts. Because spatial patterns vary with scale, field-scale and within-field spatial statistics were used to analyze patterns of *F. fusca* and TSW distribution.

Materials and Methods

***F. fusca* dispersal.** A grid of yellow, aerial traps suspended 70 cm above bare soil using clothespins on 1.59 cm diameter bamboo poles was placed in four recently disked fields of bare soil during peak spring *F. fusca* flights and left for one week. Based on previous studies, very few *F. fusca* originate from soil, even if vegetation previously present has been disked under (Barbour and Brandenburg 1994, Cho et. al 1995, Chapter 2). Therefore, captured *F. fusca* are assumed to originate from vegetation external to the fields in this study. Aerial traps consisted of 7.6 cm lengths of 2.54 cm diameter schedule 40 polyvinyl chloride (PVC) pipe spray painted yellow (Krylon Products Group, Cleveland OH) and wrapped with 101 cm^2 of stable fly sticky sleeve paper (Great Lakes IPM, Vestaburg, MI). It is apparent that the overwhelming majority of thrips captured had alighted on the trap rather than simply impacting the trap based on our observation of hundreds of sticky traps on which the ventral portion of the thrips was in contact with the trap. For this study, most traps

were placed within a rectangular grid consisting of orthogonal X- and Y-axis transects. One trap was placed at the intersection of each X-Y transect. A greater density of traps was placed closer to weedy margins to maximize the ability to detect any dispersal gradients. Additional traps were placed in non-rectangular portions of fields to cover study areas near weedy margins that were not covered by transect intersections (Figure 1). Fields I, II, and III are located in Sampson County, NC, near Newton Grove and Field IV is located in Pitt County, NC, near Greenville. Aerial traps were placed in Fields I-III on 13 May 2004, and in Field IV on 6 May 2004, at which time *F. fusca* were known to be actively dispersing from winter weed hosts. All traps remained in the vegetation-free fields for one week. *F. fusca* captured during this time were intended to be a snapshot of dispersal patterns at the beginning of peak *F. fusca* spring flights.

The aerial trap grid in Field I consisted of seven transects of four traps each and an additional 21 traps to cover non-rectangular portions of the field. Transects within the rectangular grid were located 0, 15, 29, 58, 87, and 116 m from the origin in the X direction and 20, 40, 75, and 168 m from the origin in the Y direction. The grid was bordered by weedy areas containing known *F. fusca* hosts on two sides and bare soil extending at least 45 m on the other sides (Figure 1a-d).

The trap grid in Field II consisted of seven transects with seven traps each. Transects were spaced 19 m apart in the X direction beginning at the origin, and traps within a transect were 0, 23, 81, 181, 281, 381, and 480 m from the origin in the Y direction (Figure 1 e-h). The grid was bordered on two sides by weedy areas containing known *F. fusca* hosts and

wooded land or bare soil extending at least 75 m from the grid on the other sides (Figure 1 e-h).

The trap grid in Field III consisted of seven transects in the X direction and seven traps per transect in the Y direction. Within the rectangular portion of the grid, traps were located at 93, 116, 174, 274, 374, 474, and 574 m from the origin in the Y direction and 0, 39, 77, 116, 154, 193, and 232 m from the origin in the X direction (Figure 1 i-l). An additional 10 traps were placed within the field to cover non-rectangular portions of the field bordering weedy margins (Figure 1 i-l). The grid was surrounded by bare soil on two sides extending at least 100 m, wheat, and a weedy margin containing known *F. fusca* hosts (Figure 1 i-l).

Field IV contained a trap grid with seven transects in the X direction intersecting seven transects in the Y direction except that one X transect intersected only six Y transects due to field shape (Figure 1 m-p). Transects were 36.5 m apart in the X direction and 0, 23, 58, 116, 221, 326, and 430 m from the origin in the Y direction except no trap existed at (256, 430 m). The trap grid was surrounded by at least 100 m of bare soil on two sides and wooded land on a third (Figure 1 m-p). The fourth side was bordered by a weedy ditch containing known hosts of *F. fusca*.

Thrips identification: When 25 or fewer thrips were on a trap, all thrips were identified to species. A random subsample of 25 thrips were identified when the total number of thrips exceeded 25. The proportion of *F. fusca* from the subsample was multiplied by the total number of thrips to estimate the number of *F. fusca* per trap. Thrips were mounted on

microscope slides and identified to species using a compound microscope and a key to adult thrips of the Terebrantia suborder (Palmer *et al.* 1992). Voucher specimens are held at the North Carolina State University Museum.

TSWV prevalence. In two mature tobacco fields distinct from the dispersal study fields, all tobacco plants were scored visually for TSW in every twelfth row in late July 2005. The number of infected plants per group of 50 consecutive plants was recorded as a single data point centered at the midpoint of the group, resulting in a grid of TSW prevalence across the field. At the end of each row, if fewer than 50 plants were in the final group, the number of tobacco plants was counted. Percentage of TSW infected plants was calculated for each data point.

Field V is located in Jones County, NC and was bordered on all four edges by a weedy margin ca. 2 m wide. Cotton was beyond the weedy margin on two sides and wooded land and a paved road were beyond the other two weedy edges (Figure 2 a-d). Field VI is located in Lenoir County, NC and was bordered by cotton on two sides, a weedy ditch containing *F. fusca* and TSWV hosts, and grass (Figure 2 e-h).

Data analysis. For each field, distance from the trap or TSW survey locus to the nearest weedy area (Figs. 1-2) and distance squared were regressed with *F. fusca* captured or TSW prevalence to describe spatial relationships (PROC REG) (SAS 2005). In one instance, the need for a non-polynomial model was apparent from the graph of *F. fusca* vs. distance (Figure 2, Field III). For models that cannot be expressed as a linear combination of variables, the coefficient of determination (r^2) does not have an upper bound of 1; therefore,

both the unbounded pseudo-r^2 and root mean square error (RMSE) are presented (PROC MODEL) (SAS 2005).

An interpolated surface of *F. fusca* distribution was created using the spline method in ArcGIS 9.3 to facilitate visualization of trap capture variation (ESRI 2009). Note that no statistical significance of spatial patterns can be interpreted from these images. Data for each field also were tested for clustering. At the scale of the entire grid, clustering was examined using the standardized Mantel's statistic, r_M (Manly 1986, Legendre and Legendre 1998). The Mantel's statistic is a measure of correlation between two matrices. In this study, one matrix contains the distance from each point to each other point, and the second matrix contains the difference between the number *F. fusca* captured for each pair of points. The standardized Mantel's statistic is bounded between -1 and 1 and indicates, on the whole, if the distance from weedy margins is correlated to the number of *F. fusca* captured. A negative value signifies dispersion and a positive value signifies clustering. Because each point in space is unique and therefore not replicated, p-values were estimated using the Monte Carlo method (n = 10,000 permutations) (Besag and Diggle 1977, Jackson and Somers 1989). Within-field clustering was determined using the Getis-Ord statistic, *Gi** (Ord and Getis 1995, Getis and Ord 1996). Entire-field spatial autocorrelation analysis was performed in SAS 9.1 (SAS 2005).

Within-field spatial autocorrelation can be observed as clusters of data points that have greater (hot-spot) or smaller (cold-spot) values compared to neighbors within a specified distance, *d*, than expected compared to a random distribution of the data. Because

clustering patterns change with scale, we determined the distance at which spatial clustering is most likely to be observed using the Moran's Index, *I*. Moran's *I* and its associated z-score is used to determine whether clustering, random, or disperse patterns are present within the data for a specified distance, but it does not locate areas of clustering or dispersion. One pair of *I* and associated z-score is calculated for all data points using a specified distance. The Getis-Ord statistic, *Gi(d),* and associated z-score is calculated for each point using values of neighboring points. This calculation also requires a distance input, *d*, which represents the cutoff for distance that can exist between two points that are considered neighbors. *Gi(d)* is used to determine if an individual point falls within a cluster of points constituting a statistically significant hot- or cold-spot of high or low values.

We determined the distance at which *I* was most significant for each field and used this value to calculate the *Gi(d)* value for each data point. Within a transect, let the shortest distance between two sticky traps be represented by k_{min} and the longest between two traps be $k_{max.}$ We calculated *I* and associated z-scores for the range of k_{min} to one half k_{max} using a script in ArcGIS 9.3 that was customized to iteratively compute these statistics for distances in one meter increments (ESRI 2009, Ormsby *et al.* 1999, 2008). Associated z-scores greater than 1.96 indicate autocorrelation ($\alpha = 0.05$). For *I,* significant negative z-scores indicate spatial dispersion while significant positive z-scores indicate significant clustering. For the *Gi(d)* statistic, significant negative and positive z-scores indicate cold- and hot-spots, respectively. Graphic renderings of Getis-Ord hot and cool spots were created for each field using ArcGIS 9.3 (ESRI 2009).

Results

***F. fusca* captures.** Abundant *F. fusca* were captured in Fields I-IV, and *F. fusca* dispersed across the entire length and width of the grids (Table 1). Since traps were located above bare soil, the closest source of *F. fusca* was from vegetation that was more than 400 m from some traps. Significant models were obtained using regression for Fields I-III; no significant model was obtained for field IV (Figure 3). Distance from weeds appears in regression equations for Fields I-III and the equation for Fields II contains the distance squared parameter (Figure 3). Contrary to expectations, the number of *F. fusca* captured increased with increasing distance for Field I; distance from weedy field margins accounted for 51% of observed variation (Figure 3). The model for Field II is an inverted parabola explaining 24.6% of observed variation. Similar to the linear model for Field I, an increase in number of *F. fusca* captured with increasing distance from weedy field margins was observed, but at distances greater than the parabola's vertex (48 m), the number of *F. fusca* captured decreased with increasing distance (Figure 3). The numbers of *F. fusca* captured from Field III increased with increasing distance from the weedy margin until a plateau was reached ca. 200 m from the weedy margin.

Distribution of captured *F. fusca* exhibited significant but modest whole-field correlation between the number of *F. fusca* captured and the distance to a weedy margin as described by the Mantel statistic for Fields I (r_M = 0.14) and III (r_M = 0.32) (Table 1). This indicates non-random spatial distribution of *F. fusca* captures. In contrast, significant local clustering measured by Moran's *I* and Getis-Ord statistics was observed in all fields,

indicating that spatial autocorrelation existed at a local scale even if it was not observed for the entire field (Table 1, Figure 1). The range of scale at which the most significant clustering was observed was 82 – 227 m for *F. fusca* indicating that scale of *F. fusca* clustering varies greatly among fields.

Hot- and cold-spots of captured *F. fusca* at the extremes of distance range associated with significant Moran's *I* values in comparison to the distance associated with the most significant Moran's *I* value reflect the relative stability of hot- and cold-spots over space (Figure 1). These hot- and cold-spots are often not reflected in the interpolated spline surface such as in Fields II-IV (Figure 1 e, i). Hot- and cold-spot shapes and positions are similar to each other in shape and position for Field I across the different neighbor-distances used (Figure 1 b-d), however, hot-spots are not associated with weedy margins as expected and are instead in a portion of the grid distant to thrips weed hosts. Similar shapes and positions of hot- and cold-spots show that centers of clustering or dispersion are consistent across observed spatial scales.

The hot-spots within Field II vary in shape and position between Figure 1g and Figure 1f & h. Figure 1f and h are identical, likely because the distances used to calculate Getis-Ord hot-spot values for these two images have a difference of only two meters. Hot-spots in Figure 1n & p are near a portion of the weedy margins, but hot-spots are absent near much of the weedy margins. As observed in Field I, patterns of hot- and cold-spots in *F. fusca* captured in Field III do not fit our hypothesis that more *F. fusca* would be captured closer to weedy margins and instead show that more *F. fusca* are present in the portion of the trap grid

farthest from weedy margins (Figure 1 j-l). The hot-spots found in Field IV are of similar shapes and positions across distances, indicating consistent centers of clustering and dispersion across observed spatial scales (Figure 1n-p), but the range of distances for which significant clustering was found is very small (3 m; Figure 1 n-p). The area of relatively large *F. fusca* captures is near the weedy margin and may reflect local dispersal of *F. fusca* (Figure 1 n-p).

TSWV prevalence. Final prevalence of TSW-infected tobacco plants was 14.7 and 34.7% in Fields V and VI, respectively (Table 2). Significant models were obtained for both fields, in which distance from weeds appears in each regression and the distance squared parameter is present in the model for Field VI; however, distance from weedy field margins explained only a small amount of variation in TSW prevalence (6-7%) for each field (Figure 4). The percentage of plants exhibiting TSW in Field V increased with increasing distance from weed margins (Figure 4). In contrast, the regression model for Field VI is an inverted parabola. The percentage of TSW infected plants increased with distance up until 58 meters from weedy margins after which TSW prevalence decreases with increasing distance (Figure 4). The TSW gradients in Fields V and VI were observed in mature tobacco fields distinct from fields with thrips traps, but as observed in Fields I-IV, gradients were counter to our hypothesis that more *F. fusca* and TSW would be observed closest to weedy margins.

Mantel's statistic was significant for Field V (r_M = 0.09), indicating the presence of whole-field spatial autocorrelation (Table 2). However, Mantel's statistic was not significant for Field VI (r_M = 0.05; table 2). Though whole-field spatial autocorrelation was only

observed in one of two fields, significant within-field autocorrelation was found using Moran's *I* and Getis-Ord statistics to locate hot- and cold-spots (Figure 2). The most significant clustering was observed at 76 and 48 m, respectively, for Fields V and VI.

Interpolated spline surfaces of TSW prevalence (Figure 2 a e) do not clearly reflect statistical hot- and cold-spots (Figure 2 b-d, f-h). The number, position, and shape of hot- and cold-spots changes with distance used to calculate the Getis-Ord statistics (Figure 1 b-d, f-h). These centers of statistically elevated or depressed TSW values apparently are not related to proximity with weedy borders.

Discussion

We hypothesized that more *F. fusca* would be captured on traps near field borders containing weed hosts. Additionally, if gradients of *F. fusca* captured were consistent in form (linear, quadratic, non-linear with a plateau) across fields, we expected to observe similar gradients of TSW prevalence in tobacco fields even though the fields in which *F. fusca* were captured and TSW was measured were separate. However, in three fields, fewer *F. fusca* were captured at the margin of a vegetation-free field and weedy border than were captured within the field farther away from the weedy border (Figure 1). It is unknown if the *F. fusca* captured had control over their exact flight paths; however, the observed margin effect is evidence of active alightment by *F. fusca*, indicating that the thrips are able to choose to terminate flight. Presumably, the weedy borders served as an ecological sink in *F. fusca* dispersal: either some *F. fusca* dispersing from weed hosts turned back when no suitable hosts were found nearby in the vegetation-free field while others continued to disperse

farther into the field, or *F. fusca* captured on traps originated from sources more distant than the weedy borders studied and the thrips cued in on the weed hosts rather than landing on traps when in close proximity to the weed margin. For Fields I and II, statistically significant cold-spots, which identify clusters of traps with values lower in *F. fusca* capture magnitude than expected by random chance, were observed near weedy margins (Figure 1). Although no field-scale gradient was present in Field IV (Figure 3), one hot-spot was observed (Figure 1) near the weedy field border. It is possible that the observed hot-spot, a non-uniform localized area of larger than expected *F. fusca* captures, is due to proximity to *F. fusca* weed hosts; however, our results show that proximity to thrips weed hosts is not consistently related to thrips capture numbers.

The distance at which the number of *F. fusca* captured was most significantly clustered varied from 82 to 227 m. This large range of distance indicates that the distance travelled by dispersing *F. fusca* varies from field to field. Distance travelled may be influenced by wind, which would contribute to passive dispersal, or by stimuli that influence active colonization. The variety of model types (linear, quadratic, non-linear with plateau) may also reflect that *F. fusca* dispersal is affected by factors other than distance from weedy margins. However, it is also possible that Field I covers only the linear portion of the *F. fusca* capture- distance to weedy margin relationship. Traps in Field I show increasing *F. fusca* captures with increasing distance from the weeds, but it is possible if Field I were larger, the number of *F. fusca* captured would eventually peak and then decline with increasing distance from weedy margins. The plateau observed in Field III is likely explained by the presence of

wheat, which can support populations of *F. fusca*, along the field margin distal to the weedy margin. *F. fusca* could have dispersed from the wheat as well as from the weedy margin. Alternatively, *F. fusca* that may have originated from the wheat could have dispersed toward the weedy margin, in which case the smaller numbers of *F. fusca* captured near the weedy margin still may be described by the weeds-as-a-sink hypothesis.

Distance to weedy borders explains very little variation in TSW observed in tobacco (5-6%; Table 5), and hot- and cold-spots do not occur along weedy borders (Figure 2). It is possible that cotton or weeds growing in fields prior to cotton planting served as sources of viruliferous *F. fusca* or TSW, but hot-spots do not run along field edges bordered by cotton (Figs. 2). The distances at which most significant TSW prevalence clustering was observed (76 and 48 m, respectively for Fields V and VI) are smaller than the most significant distances associated with *F. fusca* clustering. This may be because the *F. fusca* captured for this study represent a snapshot of *F. fusca* movement whereas the TSW prevalence is influenced by *F. fusca* movement and transmission. It is also possible that *F. fusca* travel shorter distances when flying over host plants rather than over bare soil. Finally, *F. fusca* dispersal patterns do not necessarily reflect feeding and TSWV transmission patterns. *F. fusca* may not feed at some alightment locations and it is known that TSWV-infected thrips do not transmit with every feeding (Rotenberg *et al.* 2009, Wijkamp and Peters 1993).

Although this study provides limited insight into the formation of exact patterns of *F. fusca* captured and TSW prevalence, it provides several important pieces of information. First, *F. fusca* can disperse at least 480 m across bare soil fields in the absence of storm

systems, which gives evidence that *F. fusca* dispersal can occur at distances greater than a field's length without the assistance of exceptional weather. Second, our findings indicate that distant (non-field margin) sources of *F. fusca* and TSW may be important to the spatial distribution of both vector and disease. Local management of *F. fusca* and TSW weed hosts in naturally occurring vegetation around field margins may have limited impact on TSW incidence in adjacent fields in eastern NC for which *F. fusca* is the primary vector. Third, since *F. fusca* are able to actively initiate and terminate dispersal and travel long distances, dispersal patterns will be affected by land cover beyond a field of interest and its immediate surroundings. Therefore, in regions such as NC that have high crop diversity, *F. fusca* dispersal patterns are likely affected by host-preference relationships.

References Cited

Barbour, J. D. and R. L. Brandenburg. 1994. Vernal infusion of thrips into North Carolina peanut fields. J. Econ. Entomol. 87: 446-451.

Besag, J. and P. J. Diggle. 1977. Simple Monte Carlo tests for spatial pattern. *Appl. Statist.* 26: 327-333.

Cho, K. C., S. Eckel, J. F. Walgenbach, and G. G. Kennedy. 1995. Overwintering of thrips (Thysanoptera: Thripidae) in North Carolina. *Environ. Entomol.* 24: 58-67.

Collinge, S. K. and S. M. Louda. 1989. Influence of plant phenology on the insect herbivore/bittercress interaction. *Oecologia*. 79: 111-116.

Coutts, B.A., M.L. Thomas-Carroll, and R.A.C. Jones. 2004. Patterns of spread of tomato spotted wilt virus in field crops of lettuce and pepper: spatial dynamics and validation of control measures. *Annals of Applied Biology.* 145: 231-245.

Crone, E. E. and C. G. Jones. 1999. The dynamics of carbon-nutrient balance: effects of cottonwood acclimation to short- and long-term shade on beetle feeding preferences. *J. Chem. Ecol.* 25: 635-56.

ESRI (Environmental Systems Research Institute). 2009. ArcGIS software, version 9.1.3. ESRI. Redlands, CA.

Getis, A. and J. K. Ord. 1996. Local spatial statistics: and overview. p. 261-71. *in* P. Longley and M. Batty [eds.]. Spatial Analysis: Modeling in a GIS Environment. GeoInformation International, Cambridge.

Grevstad, F. S. and A. L. Herzig. 1997. Quantifying the effects of distance and conspecifics on colonization: experiments and models using the loosestrife leaf beetle, *Galerucella calamariensis*. 110: 60-68.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2001. Overwintering of *Frankliniella fusca* (Thysanoptera: Thripidae) on winter annual weeds infested with tomato spotted wilt virus and patterns of virus movement between susceptible hosts. *Phytopathol.* 91: 891-899.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2002. The role of weed hosts and tobacco thrips, *Frankliniella fusca*, in the epidemiology of tomato spotted wilt virus. *Plant Disease* 86: 573-582.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2003. Seasonal dispersal patterns of *Frankliniella fusca* (Thysanoptera: Thripidae) and tomato spotted wilt virus occurrence in central and eastern North Carolina. *J. Econ. Entomol.* 96: 1-11.

Hanski, I. M. Huussaari and M. Nieminen. 1994. Metapopulation structure and migration in the butterfly *Melitae cinxia*. *Ecology*. 75: 747-762.

Iason, G. R. and A. J. Hester. 1993. The response of heather (*Calluna vulgaris*) to shade and nutrients-predictions of the carbon-nutrient balance hypothesis. *J. Ecol.* 81: 75-80.

Jackson, D. A. and J. M Somers. 1989. Are probability estimates from the permutation model of Mantel's test stable? *Canadian J. Zool.* 67: 766-769.

Jones, R. E. 1977. Movement patterns and egg distribution in cabbage butterflies. *J. Anim. Ecol.* 46: 195-212.

Legendre and Legendre 1998. Numerical ecology, 2nd ed. Vol. 20 Developments in environmental modeling. Elsevier Science. 870 p.

Lewis, T. 1969. The distribution of flying insects near a low hedgerow. *J. Appl. Ecol.* 6: 443-452.

Lewis, T. 1970. Patterns of distribution of insects near a windbreak of tall trees. *Ann. Appl. Biol.* 65: 213-220.

Lewis, T. and J. W. Stephenson. 1966. The permeability of artificial windbreaks and the distribution of flying insects in the leeward sheltered zone. *Ann. Appl. Biol.* 58: 355-363.

Manly, B.F.J. 1986. Randomization and regression methods for testing for associations with geographical, environmental and biological distances between populations. *Researches on Population Ecology*. 28: 201-218.

Moran, P. A. P. 1950. Notes on continuous stochastic phenomena. *Biometrika*. 37: 17-23.

Morsello, S. C., R. L. Groves, B. A. Nault, and G. G. Kennedy. 2008. Temperature and precipitation affect seasonal patterns of dispersing tobacco thrips, *Frankliniella fusca*, and onion thrips, *Thrips tabaci* (Thysanoptera: Thripidae) caught on sticky traps. Envrion. Entomol. 37: 79-86.

Morsello, S. C., A. L. P. Beaudoin, R. L. Groves, B. A. Nault, and G. G. Kennedy. 2010. The influence of temperature and precipitation on spring dispersal of *Frankliniella fusca* changes as the season progresses. *Entomol. Exp.Appl.* 134: 260-271.

Ord, J. K. and A. Getis. 1995. Local spatial autocorrelation statistics: distributional issues and an application. *Geographical Analysis*. 27: 286-306.

Ormsby, T. J., E. Napoleon, and R. Burke. 2008. Getting to know ArcGIS desktop: the basics of ArcView, ArcEditor, and ArcInfo updated for ArcGIS 9, 2nd ed. ESRI Press: Redlands, CA. 592 p.

Palmer, J. M., L. A. Mound, and G. J. du Haeume. 1992. IIE guides to insects of importance to man, vol. 2. Thysanoptera (ed. by CR Betts), pp. 73. International Institute of Entomology, CAB International, Wallingford, UK.

Pasek, J. E. 1988. Influence of wind and windbreaks on local dispersal of insects. *Agriculture, Ecosystems and Environment*. 22/23: 539-554.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*. 43: 95-124.

Rotenberg, D., N. K. K. Kumar, D. E. Ullman, M. Montero-Astua, D. K. Willis, T. L. German, and A. E. Whitfield. 2009. Variation in *tomato spotted wilt virus* titer in *Frankliniella occidentalis* and its association with frequency of transmission. *Phytopath.* 99: 404-410.

SAS Institute, Inc. 2005. SAS® 9.1.3 Intelligence Platform: Single-User Installation Guide. Cary, North Carolina, USA.

Stein, S. J., P. W. Price, T. P. Craig, and J. K. Itami. 1994. Dispersal of a galling sawfly: implications for studies of insect populations. *J. Animal Ecol.* 63: 666-676.

Taylor, L. R. 1974. Insect migration, flight periodicity and the boundary layer. *J. Animal Ecol.* 43: 225-238.

Trichilo, P. J. and T. F. Leigh. 1986. Predation on spider mite eggs by the western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), an opportunist in a cotton agroecosystem. 15: 821-825.

Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leasing dimensions of variation between species. *Annu. Rev. Ecol. Syst.* 33: 125-59.

Whitfield, A.E., D.E. Ullman, and T.L. German. 2005. Tospovirus-thrips interactions. *Annu. Rev. Phytopathol.* 43: 459-489.

Wijkamp, I. and D. Peters. 1993. Determination of the median latent period of two tospoviruses in *Frankliniella occidentalis*, using a novel leaf disk assay. *Phytopathology.* 83: 986-991.

Wilson, L. and R. Morton. 1993. Seasonal abundance and distribution of *Tetranychus urticae* (Acari, Tetranychidae), the 2 spotted spider-mite, on cotton in Australia and implications for management. *Bulletin Entomological Research.* 83: 291-303.

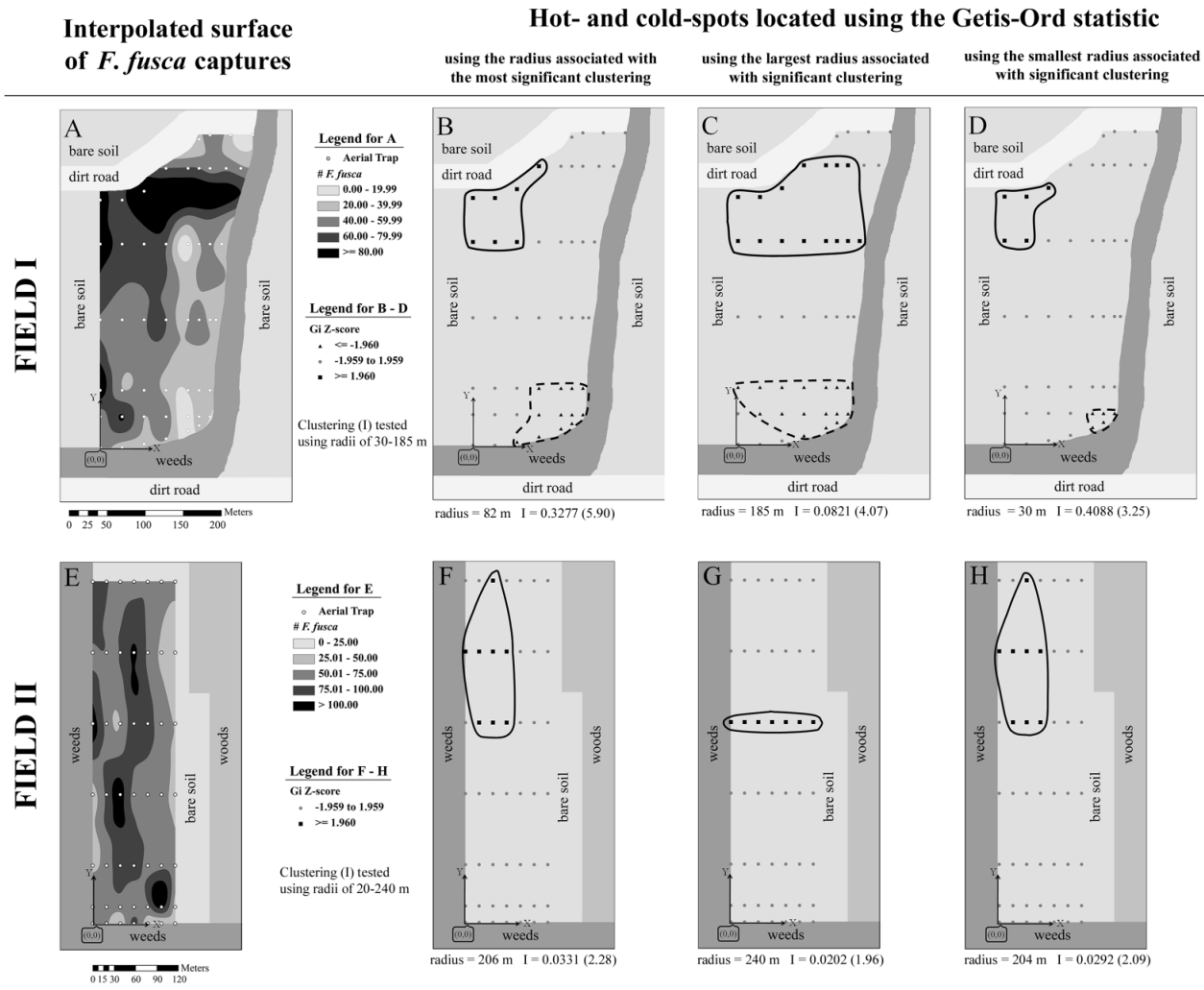
Table 1. Summary and Mantel (r_M) statistics for the number of *F. fusca* captured on a grid of sticky traps in each field. Significant p-values corresponding to r_M indicate presence of whole-field spatial autocorrelation. Significant r_M and associated p-values are bold.

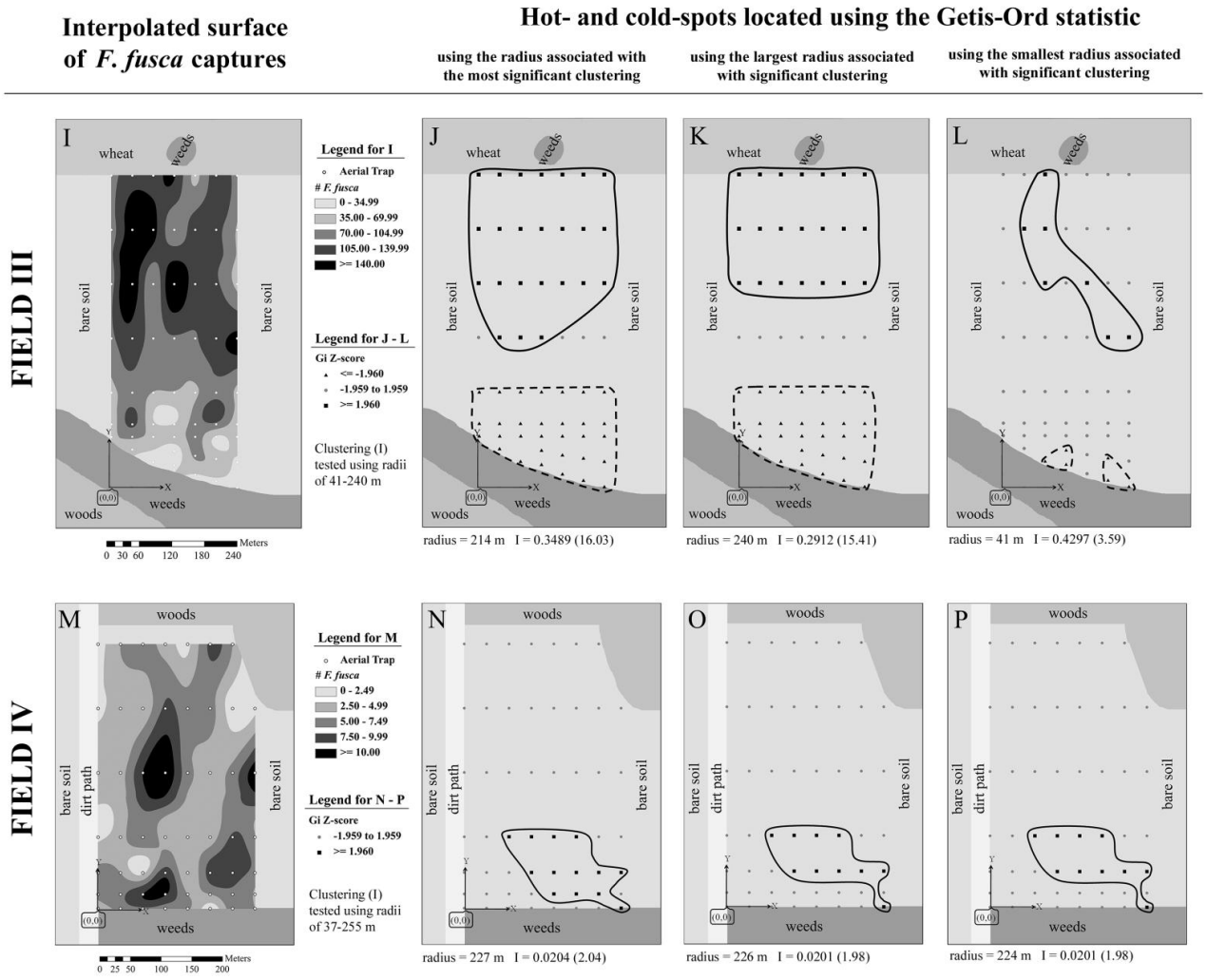
Field	# of traps	Mean	Variance	Minimum	Maximum	r_M	p-value
A	49	47.6	515.2	5.9	99.2	**0.1372**	**0.009**
B	49	65.2	466.4	19.8	115.1	-0.0022	0.974
C	59	81.8	1590.6	11.0	174.8	**0.3190**	**< 0.0001**
D	55	5.5	7.0	1.0	12.0	0.1131	0.3868

Table 2. Summary and Mantel (r_M) statistics for the percentage of tobacco plants exhibiting TSW symptoms in each mature tobacco field. Each data point represents the percentage of plants showing TSW symptoms out of 50 consecutive plants within a row. Significant p-values corresponding to r_M indicate presence of whole-field spatial autocorrelation. Significant r_M and associated p-values are bold.

Field	# Data points	Mean	Variance	Minimum	Maximum	r_M	p-value
E	96	14.7	37.5	0.0	32.0	**0.0948**	**0.0266**
F	70	34.7	96.5	13.5	58.0	0.0470	0.2058

Figure 1. Sticky traps were suspended above bare soil to study the *F. fusca* dispersal pattern from natural weed hosts. Each shape-point represents one trap. The trap grid is to scale but adjacent land cover is not. Bare soil extended at least 45 and 75 m from the trap grids in Fields I and II, respectively, and at least 100 m from the trap grid in Fields III and IV. Statistical *F. fusca* hot- and cold-spots are circled by solid and dashed lines, respectively. For each field, the hot-and cold-spots on the three right-most images were created using the search radius indicated below the image. Moran's *I*, which measures clustering, is indicated after the radius and the associated z-score is follows in parentheses.


Interpolated surface of F. fusca captures
Hot- and cold-spots located using the Getis-Ord statistic
using the radius associated with the most significant clustering
using the largest radius associated with significant clustering
using the smallest radius associated with significant clustering
FIELD I
FIELD II
A
B
C
D
E
F
G
H
bare soil
dirt road
weeds
woods
Legend for A
Aerial Trap
F. fusca
0.00 - 19.99
20.00 - 39.99
40.00 - 59.99
60.00 - 79.99
>= 80.00
Legend for B - D
Gi Z-score
<= -1.960
-1.959 to 1.959
>= 1.960
Clustering (I) tested using radii of 30-185 m
Legend for E
Aerial Trap
F. fusca
0 - 25.00
25.01 - 50.00
50.01 - 75.00
75.01 - 100.00
> 100.00
Legend for F - H
Gi Z-score
-1.959 to 1.959
>= 1.960
Clustering (I) tested using radii of 20-240 m
Meters
0 25 50 100 150 200
0 15 30 60 90 120
radius = 82 m I = 0.3277 (5.90)
radius = 185 m I = 0.0821 (4.07)
radius = 30 m I = 0.4088 (3.25)
radius = 206 m I = 0.0331 (2.28)
radius = 240 m I = 0.0202 (1.96)
radius = 204 m I = 0.0292 (2.09)


Interpolated surface of F. fusca captures
Hot- and cold-spots located using the Getis-Ord statistic
using the radius associated with the most significant clustering
using the largest radius associated with significant clustering
using the smallest radius associated with significant clustering
FIELD III
FIELD IV
I
J
K
L
M
N
O
P
wheat
weeds
woods
bare soil
dirt path
Legend for I
Aerial Trap
F. fusca
0 - 34.99
35.00 - 69.99
70.00 - 104.99
105.00 - 139.99
>= 140.00
Legend for J - L
Gi Z-score
<= -1.960
-1.959 to 1.959
>= 1.960
Clustering (I) tested using radii of 41-240 m
Meters
0 30 60 120 180 240
radius = 214 m I = 0.3489 (16.03)
radius = 240 m I = 0.2912 (15.41)
radius = 41 m I = 0.4297 (3.59)
Legend for M
0 - 2.49
2.50 - 4.99
5.00 - 7.49
7.50 - 9.99
>= 10.00
Legend for N - P
Clustering (I) tested using radii of 37-255 m
0 25 50 100 150 200
radius = 227 m I = 0.0204 (2.04)
radius = 226 m I = 0.0201 (1.98)
radius = 224 m I = 0.0201 (1.98)

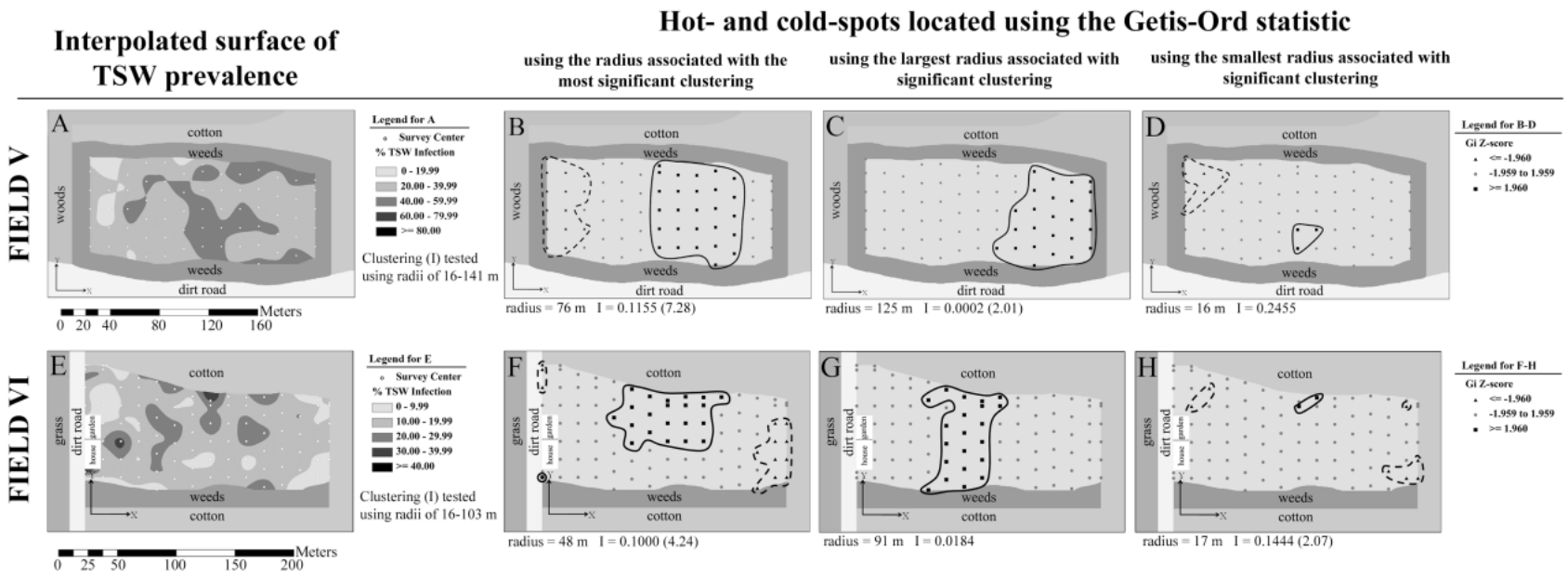


Figure 2. Each shape-point represents the percentage of mature tobacco plants exhibiting TSW symptoms within each consecutive sample. The grid is to scale but adjacent land cover is not. Statistical TSW hot- and cold-spots are circled by solid and dashed lines, respectively. For each field, the hot-and cold-spots on the three right-most images were created using the search radius indicated below the image. Moran's *I*, which measures clustering, is indicated after the radius and the associated z-score is follows in parentheses.

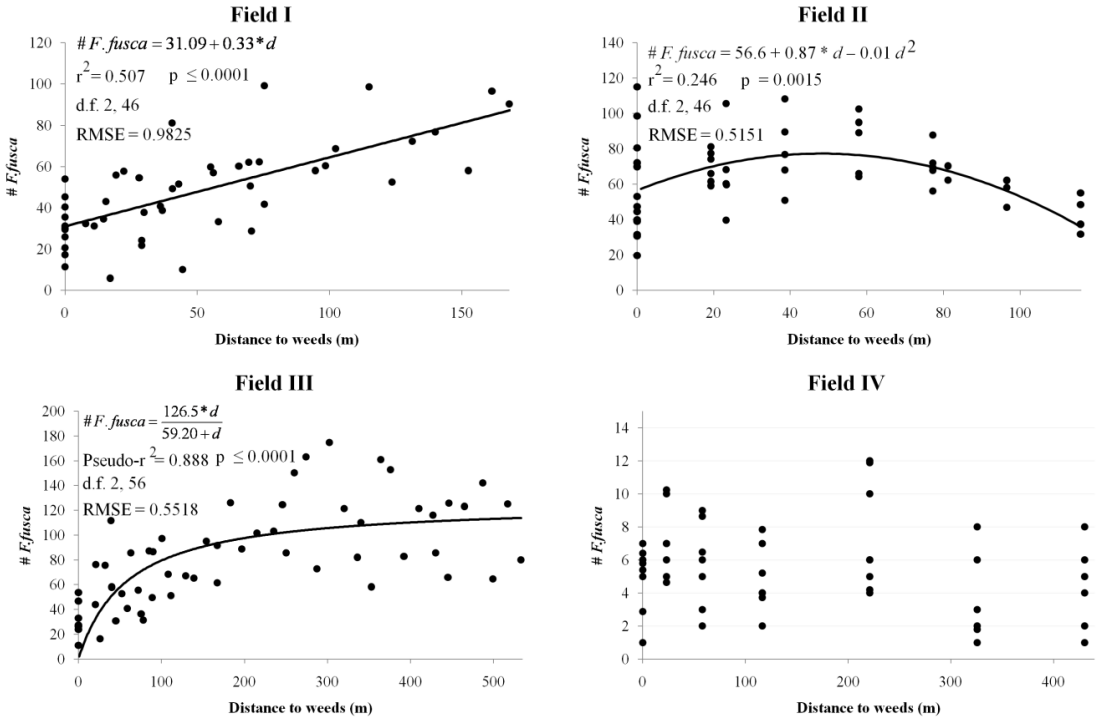


Figure 3. Regression of number of *F. fusca* per sticky trap in a recently disked field with distance (*d*) to *F. fusca* weed hosts. Individual points indicate actual number of *F. fusca* captured per trap. No regression model was significant for Field IV.

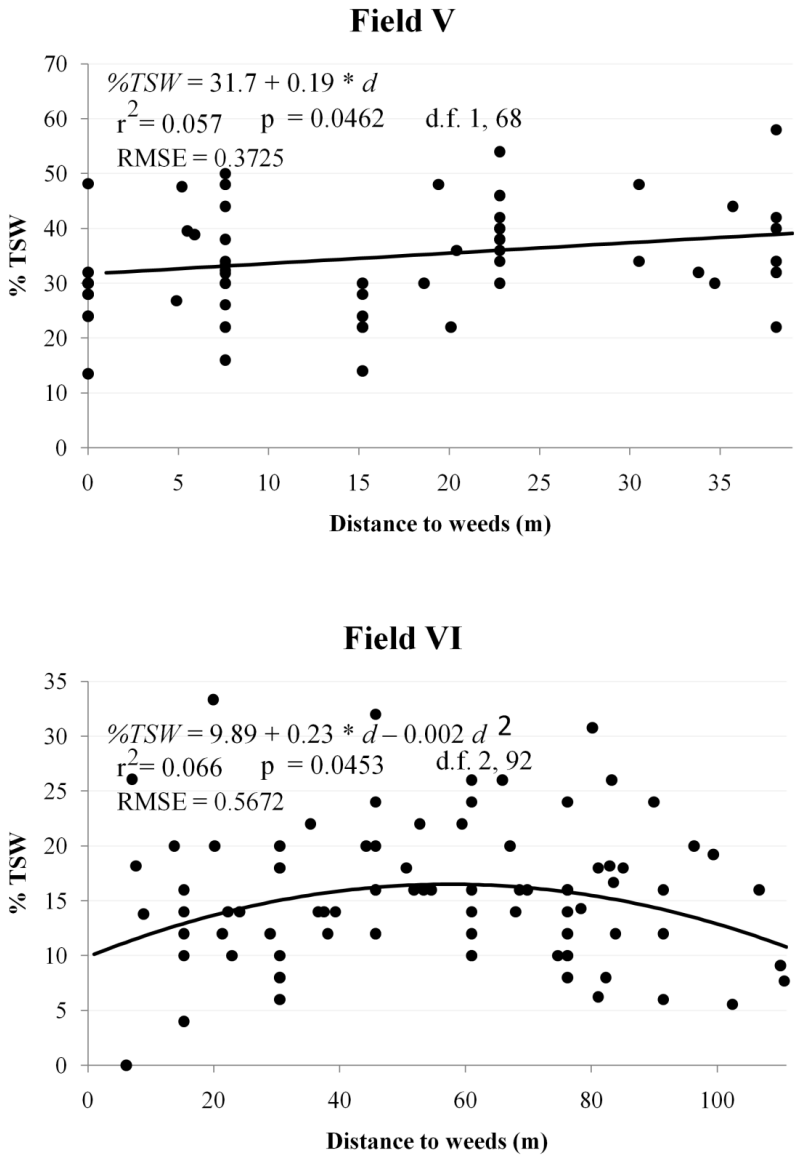


Figure 4. Regression of percentage of mature tobacco plants exhibiting TSW symptoms with distance (*d*) to *F. fusca* weed hosts. Individual points indicate percentage of tobacco within each sample of consecutive plants exhibiting TSW symptoms.

CHAPTER 4

Assessment of the potential for secondary spread of tomato spotted wilt virus in tomato and pepper fields based on in-depth observations of *Frankliniella fusca* (Hinds) and *F. occidentalis* (Pergande) throughout the growing season

Abstract

Tomato spotted wilt virus (family Bunyaviridae, genus *Tospovirus*, TSWV) affects many crops including tomato, pepper, peanut, and tobacco and is exclusively transmitted by several species of thrips. The tobacco thrips, *Frankliniella fusca*, and the western flower thrips, *F. occidentalis*, are considered the most important vector species in the southeastern United States. Primary transmission of TSWV occurs when adult thrips vectors disperse from senescing winter weed hosts to summer annual weeds and crops in late spring. Repeated observations of tomato and pepper fields surrounded by minimal weedy margins that could serve as TSWV reservoirs and yet had high end-of-season TSW prevalence raised the question of whether or not secondary spread of TSWV might be occurring in North Carolina. To more completely understand TSW spread in tomato and pepper fields in North Carolina, the following questions were studied: 1. What thrips vector species are present within tomato and pepper fields? 2. Are thrips vectors from the tomato and pepper fields able to transmit TSWV? 3. Does sufficient developmental time pass from the initial observation of TSW infection to plant harvest for thrips to develop on infected plants and for secondary spread to occur? and 4. Can data about TSW diseased tomato and pepper plants over time and space be used to understand whether a non-diseased tomato or pepper plant will become infected? Sticky trap, foliage, and blossom data indicate that *F. fusca* are transient and do not establish resident populations within tomato and pepper fields, but *F. occidentalis* colonizes at least some fields of both crops. Transmission assays using thrips vectors collected from within tomato and pepper fields indicate that some *F. occidentalis* acquire TSWV from infected

plants within the field and are competent vectors, potentially contributing to secondary spread. Evidence of secondary spread within tomato fields was revealed by regression models, and the potential for secondary spread within pepper field exists.

Introduction

For any plant-insect-pathogen system, a basic understanding of how and when a pathogen is transmitted from vector to host plant provides fundamental epidemiological knowledge. Insect-borne virus transmission to crops by vectors that acquire the pathogen external to the field is primary spread. Secondary spread is transmission of the virus from a source internal to the crop field. Many insects including aphids and leafhoppers are responsible for secondary spread of plant viruses within crops (ex. Chancellor et al. 1996, Atiri et al. 1986). *Tomato spotted wilt virus* (family Bunyaviridae, genus *Tospovirus*, TSWV) is the causative agent of the disease tomato spotted wilt (TSW), which affects many crops including tomato, pepper, peanut, and tobacco (Whitfield et al. 2005). TSWV is transmitted exclusively by several species of thrips, including the tobacco thrips, *Frankliniella fusca* (Hinds), and the western flower thrips, *F. occidentalis* (Pergande), which are considered the most important vector species in the southeastern United States (Eckel et al. 1996, Groves et al. 2003, Whitfield et al. 2005). Groves et al. indicated that *F. fusca* is likely the main vector species of TSWV in North Carolina based on thrips sticky trap data collected from field margins, especially early in the growing season (2003). Within-field samples by Eckel et al. suggest that *F. fusca* as well as *F. occidentalis* are likely important vectors in tomato and pepper (1996).

Thrips vector species can transmit TSWV only if they acquire the virus as first instars, but thrips infected as first instars can transmit throughout adulthood (Linford 1962, Sakimura 1962, van de Wetering et al. 1996). Because a thrips must acquire TSWV as a first instar and mobility at this stage is very limited, thrips vector species must hatch on previously infected plants in order to acquire TSWV. Although second instar larvae are able to transmit TSWV (Wijkamp and Peters 1993), limited mobility minimizes the opportunity of second instar larvae to infect healthy plants. Additionally, thrips pre-pupae and pupae are non-feeding stages, so thrips vectors do not transmit TSWV at these stages. The overwhelming majority of TSWV transmission is by thrips adults. In the late winter and early spring, thrips populations and TSWV inoculum increase in winter annual and perennial weed hosts. Primary transmission of TSWV occurs when adult thrips vectors disperse from senescing winter weed hosts to summer annual weeds and crops in late spring (Eckel et al. 1996, Groves et al. 2003, Kahn et al. 2005).

Studies evaluating whether or not secondary spread of TSWV occurs have concluded that secondary spread does not occur or is limited in peanut (Camann et al. 1995), lettuce (Coutts 2004), tomato and pepper (Gitaitis et al. 1998). However, repeated personal observations (Amanda Beaudoin and George Kennedy) of tomato and pepper fields with 40-90% end-of-season TSW prevalence surrounded by minimal weedy margins that could serve as TSWV reservoirs raised the question of whether or not secondary spread of TSWV might be occurring in North Carolina. Gitaitis et al. (1998) did not sample thrips from tomato and pepper fields in which they studied secondary spread of TSW. To obtain a more complete

understanding of TSW spread in tomato and pepper fields in North Carolina, the following questions were studied: 1. What thrips vector species are present within tomato and pepper fields? 2. Are thrips vectors from the tomato and pepper fields able to transmit TSWV? 3. Does sufficient developmental time pass from the initial observation of TSW infection to plant harvest for thrips to develop on infected plants and for secondary spread to occur? and 4. Can data about TSW diseased tomato and pepper plants over time and space be used to understand whether a non-diseased tomato or pepper plant will become infected?

Materials and Methods

Plot Setup. Plots of 500 to 1000 plants susceptible to TSW within commercial tomato and pepper fields were observed and sampled every other week for TSW and thrips vectors throughout a growing season. Data were collected from two plots per field with the exception of one field that was too small for multiple plots. When data were obtained from two plots per field, the plots were designated “A” and “B.” Plots were separated by a minimum of 30 rows and all plot row-ends were at least 15 m from the field-edge (Figure 1). However, usable data were obtained from only one plot per field in four fields due to the presence of multiple varieties within a plot or because storm damage made a complete set of observations impossible. All but one plot consisted of 10 rows, and each plot-row contained either 50 plants (single-bedded rows) or 100 plants (double-bedded rows), though the entire row contained many more plants. All plots of 10 rows contained one row along a field edge. The remaining plot was six rows wide, and each row within the plot-area contained 165 plants and had two rows along a field edge.

In 2006, plots were observed in four tomato fields. Fields 1-3 were comprised of grape tomato plants and were located on the same farm in Faison, NC (Duplin County). Fields were 300-500 m apart. Field 4 was located near Spivey's Corner, NC (Sampson County) and was planted with fresh market tomato plants. In 2007, all three tomato fields (Fields 5-7) were located on the same farm as Fields 1-3 from the previous year. Fields 5-7 were 300-1200 m apart and planted with grape tomato plants. In both years, all tomatoes were staked and grown on black mulch.

In 2006, the three of four sweet bell pepper fields (Fields 8, 9, and 11) were located near Clinton, NC (Sampson County). Field 10 was near Delway, NC (Sampson County). All pepper fields were planted in bare soil in 2006. The three sweet bell pepper fields (Fields 12-14) and the banana pepper field (Field 15) observed in 2007 were located near Clinton, NC. Fields 12 and 13 were doubled bedded and planted in black mulch. Fields 14 and 15 were planted in bare soil. Table 1 contains specific field characteristic information, including row and plant spacing for each plot.

TSW Data Collection. Each plant within a plot was visually scored for TSW symptoms every other week beginning ca. 4-6 weeks post transplant in 2006 and ca. 1-3 weeks post transplant in 2007. If the date of transplant was unknown, 15 April was assumed as the transplant date. In 2006, all plants showing TSW symptoms were confirmed by a commercially DAS-ELISA kit (Agdia Inc., Elkhart, IN) through 20 June 2006. After this time, up to 25 newly symptomatic plants per plot were sampled and confirmed to be infected with TSWV each sample period except for the last sample period, for which all newly

symptomatic plants were confirmed using DAS-ELISA. It was necessary to subsample symptomatic plants due to financial and time constraints. In 2007, all symptomatic plants were confirmed using DAS-ELISA through 13 June 2007. Visual scoring accuracy for subsamples was 95% for tomato and 92% for pepper. Four control samples from tomato or pepper plants grown in a TSWV-free greenhouse were assayed for each DAS-ELISA performed. Any plant with an absorbance reading of more than the average plus four standard deviations of the control plants was considered positive for TSWV. The spatial position of each plant was recorded, and in 2007, dead plants were also tracked. In 2007, plant stand counts used to determine the percentage of plants with TSW was based on the number of living plants recorded on the first sample period during which TSW was first observed. For 2006, since plant death was not tracked, plant stand counts were considered to be 500 plants (no dead plants) except for Field 4 which had 990 plants (Table 1).

Sticky Trap Data Collection. Clear plastic (5 mm Vivak plastic: AIN Plastics, Greensboro, NC) was cut to 5.1 x 5.1 cm cards that were spay painted yellow (Krylon Products Group, Cleveland OH) and wrapped with 38.7cm^2 of clear stable fly sticky sleeve paper (Great Lakes IPM, Vestaburg, MI) such that both sides of a card contained a sticky surface. Fifteen pairs of cards were attached to bamboo poles using wooden clothes pins and were placed within each plot indicated in Table 1. The cards were paired such that, in relation to a given field, directional thrips data (not presented here) could be collected. For each trap, one of the cards was oriented perpendicular to field rows, and the other card was parallel to the rows. Five cards were evenly spaced within a row and sticky traps were always placed in

a row along the edge of the field (Figure 1). Sticky traps were placed just above the plant canopy and adjusted upward each sample period to maintain the trap at canopy height. Because processing each pair of cards for all 16 plots for which traps were collected during a season would require an impractical amount of labor for extraction and identification from each of four surfaces, eight of the sticky trap cards that were placed perpendicular to rows and seven of the cards placed parallel to rows were considered in this study. If any of the traps designated for processing were missing, the nearest trap within that row with the same orientation relative to a row was processed instead.

In 2007, four sticky traps were placed around the margins of three tomato and three pepper fields (Table 1). One sticky trap was along each field border, and sticky traps were a minimum of 75 m apart. Only one set of four external sticky traps was placed around each field, even if the field contained two plots. The external traps were comprised of 7.6 cm lengths of 2.54 cm diameter schedule 40 polyvinyl chloride (PVC) pipe sprayed with the same yellow paint as the directional traps and wrapped with 55.7 cm^2 of stable fly sticky sleeve paper. These external-to-the-field traps were suspended using a wooden clothes pin on a bamboo pole 0.7 m above the ground- a height at which dispersing thrips are known to be captured (Groves et al. 2003).

Thrips Identification. For each external sticky trap or side of a sticky card, all thrips were counted, and all thrips were identified to species if 25 or fewer thrips were on the trap. If more than 25 thrips were present on a trap, a random subsample of 25 of thrips was excised from the sticky trap. The proportion of vector species from the subsample was

multiplied by the total trap count to obtain an estimate of the number of each vector species captured on the trap. Thrips were identified to species using a compound microscope and a dichotomous key to the species of adult thrips within the suborder Terebrantia (Palmer et al. 1992). Voucher specimens are held at the North Carolina State University Insect Museum. Thrips sticky trap data presented in graphs are in thrips per day due to slight variations in the number of days between sample periods caused by inclement weather.

Thrips Census on Plants. In 2007, foliage and blossoms within each plot were sampled for presence of vector species of thrips. For a given sample date, foliage and blossom samples were collected from plants with TSW symptoms when possible. For each plot, 10 foliage and 5 blossom samples were collected each sample period. Foliage samples consisted of 0.1-8.4g of new plant-growth material (dry weight), and samples typically weighed 1-3 g. Smaller samples were necessarily collected when plants were young. Infected plants for sampling were chosen randomly. All thrips data from foliage samples presented were standardized to 5g of dry weight foliage. In the event that five or 10 infected plants were not available to sample for blossoms and foliage, respectively, all infected plants were sampled and the remainder of the samples were taken randomly from asymptomatic plants. Blossom samples consisted of either 10 tomato flowers from one plant or 5 pepper flowers from one plant. All sampled blossoms were open at the time of collection. Blossoms were sampled from half of the same plants from which foliage samples were collected.

Each foliage or blossom sample was placed in a 474 ml plastic cup (Sweetheart Cup Co., Inc., Chicago, IL) with Bedbug 110 mesh (183 x 183 µm openings, 52% open)

(Greenthumb Group, Downer's Grove, IL) screened lids. A *Phaseolus vulgaris* L. bean pod was placed within each cup and samples were placed within a dehumidifying chamber at 27°C and ca. 25% R.H. As the foliage or blossoms desiccated, the thrips moved to the bean pod. Samples were held for three days, at which time all adult thrips were collected into 70% ethanol alcohol. All adult thrips were counted and up to 25 thrips were mounted on a slide using CMC-10 mounting media (Masters Chemical Co., Elk Grove, IL) and identified to species. The total number of vectors was estimated as previously described. Any immature thrips were reared for an additional 7 days, allowing development to adulthood without allowing sufficient time for any eggs laid by field-collected adults to mature to adulthood. Rearing of immature thrips to adulthood was necessary because identification keys are only available for adult thrips. If the field-collected immature thrips were from a TSW-symptomatic plant, the thrips were used in a TSWV transmission assay and subsequently identified to species. Otherwise, thrips were transferred to 70% ethanol and identified as previously described.

Transmission Assays. Only thrips collected from plots as immature insects on infected plants were used in the transmission assays because thrips can only acquire TSWV as first instars, and a field-collected adult thrips could have hatched on either an infected or uninfected plant before moving to the infected plant from which it was collected. Due to their limited mobility, immature thrips most likely hatched on the infected plants from which they were collected. After the field-collected immature thrips became adults, insects were placed individually using a fine-tipped paint brush onto 1 cm diameter petunia (*Petunia hybrida* L.,

cv. “Celebrity Blue”) leaf disks that were inserted into 1.5 ml microcentrifuge tubes (Fisher Scientific, Rochester, NY) (Wijkamp and Peters 1993). The petunia leaf disks were removed from the tubes and held on moist filter paper (Fisher Scientific, Rochester, NY) in 10 cm diameter Petri dishes for five days. Leaf disks were then subjected to DAS-ELISA as previously described. Control petunia plants were maintained in a TSWV-free greenhouse.

Expected Adult Generation Turnover Dates. For secondary spread of TSWV to occur, thrips vector species must oviposit in infected plants and first instar thrips must acquire TSWV from the infected host plant. The progeny must become adults before they are mobile enough to contribute significantly to secondary spread. The timing of thrips development to adulthood can be predicted by using degree-day model calculations. Lowry et al. (1992) determined that *F. fusca* develop from egg to adult in 234.1 degree-days and have a lower developmental threshold of 10.5°C. *F. occidentalis* develop from egg to adult in 253.9 degree-days and have a lower developmental threshold of 6.5°C. TSW symptoms take a minimum of one week to appear after initial plant infection. Therefore, the degree-day accumulation start-date was one week prior to the first sample date on which TSW was observed for a given plot. Using weather data available from the National Oceanic and Atmospheric Administration (NOAA) (http://cdo.ncdc.noaa.gov/dly/DLY), the half-sine method of degree-day calculation developed by Higley et al. (1986), and the SAS code developed by Morsello et al. (2010), the date on which progeny from infected plants became adults that could potentially contribute to secondary spread was estimated.

Data Analysis. Sticky traps internal and external to a field were compared using repeated measures analysis in PROC MIXED using SAS 9.1 (SAS Institute, 2005). PROC MIXED was used instead of PROC GLM for repeated measures analysis because PROC MIXED is better able to handle missing data. Within each week, contrast analysis between internal and external traps was performed. Because the area of sticky sleeve varied between the external and internal traps, the number of thrips captured on an internal sticky card was multiplied by 1.44 to standardize the sticky area of the internal card area to that of the external trap.

If secondary spread occurs in a field, it is reasonable to expect a relationship between whether or not a plant becomes diseased and the number and distance of neighboring diseased plants during previous sample periods. Stepwise regression analysis within PROC LOGISTIC (SAS Institute 2005) was used to relate change in TSW infection status (asymptomatic to symptomatic) to the weighted or unweighted number of diseased neighbors from previous sample periods. For the unweighted representation of diseased neighbors, each diseased neighbor had a value equal to any other diseased neighbor representing its relative influence to change an asymptomatic neighbor to a diseased neighbor. Weighting of a diseased plant's influence on a susceptible neighbor was represented by an insect dispersal model since it is expected that TSW within a field will reflect insect dispersal patterns. Although many insect dispersal models were used to search for models indicating secondary spread of TSW, similar results were found across models and only the Cauchy probability distribution model is presented. The additional insect dispersal models that were tested but

are not presented here relate the number of insects captured (dependent variable) to the following representations of independent variables:

$\frac{c}{distance}, \frac{c}{distance^2}, \frac{c}{\sqrt{distance}}$, and $e^{-c*distance}$, where *c* is a constant. With respect to insects captured at a distance from a source point, the Cauchy probability distribution model is:

$$\#insects = \frac{c}{(\pi\ \text{distance}_{\text{median}})\left(1 + \frac{\text{distance}_{ij}}{\text{distance}_{\text{median}}}\right)^2}$$

where $\text{distance}_{\text{median}}$ is the median distance of all insect captures, distance_{ij} is the distance from source point *i* to point *j*, and *c* is a constant. Mayer and Atzeni (1993) found the Cauchy probability distribution to be a good fit for the primary screwworm fly, *Cochliomyia hominivorax* (Coquerel) because the model has a zero slope at the point of origin, a shape that describes catches of insects very near the origin point with the insect captures rapidly decreasing with distance from the origin point but with a long tail that realistically describes the habit of some individuals to disperse longer distances. Because it is known that *F. occidentalis* captures on sticky traps increase with proximity to weed hosts (Groves et al. 2001) and *F. fusca* can disperse from weedy hosts for hundreds of meters (Chapter 3), a model that allows for short and longer dispersal was chosen for presentation.

If one assumes that TSW spread reflects dispersal of thrips vectors, a change in disease status (asymptomatic to symptomatic) can be associated with the influence of diseased neighbor plants using a distance-weighted (Cauchy) or equal-weighted (simple count of diseased plants) model. Plants *i* and *j* are considered neighbors if the distance between the plants is less than or equal to the distance spanned by a given number of row-

spaces, $dist_{rs}$. Let these equations used to calculate parameters be considered the "unmodified" distance-weighted (Cauchy) and equal-weighted (simple count) neighbor base models. For each asymptomatic or newly symptomatic plant within a given plot, the number of diseased neighboring plants, total number of neighboring plants, distance to each diseased neighbor, and median distance to diseased neighbors was calculated for every combination of each multiple of row-spaces from one to total number of rows minus one at each previous sample period. For example, if a plot contains 10 rows, and calculations are performed for the third sample period, diseased and total neighbors were found during sample periods one and two at each row-space multiple from one to nine. For each sample period – row space combination, the neighbor data for each plant was then summed as follows:

$$\sum_{j}^{n} \begin{cases} 0 \ if \ neighbor \ j \ is \ asymptomatic \\ 1 \ if \ neighbor \ j \ is \ diseased \end{cases}$$

where the summation represents the equal-weight simple count model, and *j* through *n* represent all neighbors of plant *i*, and,

$$\sum_{j}^{n} \begin{cases} 0 \ if \ neighbor \ j \ is \ asymptomatic \\ \dfrac{1}{(\pi \ distance_{median}) \left(1 + \dfrac{distance_{ij}}{distance_{median}}\right)^2} \ if \ neighbor \ j \ is \ diseased \end{cases}$$

represents the summation for the distance-weight Cauchy model.

Both the simple count and Cauchy neighbor summations were further explored with the following modifications: 1. Corrected for plot edges and 2. Divided by the natural log of the product of number of neighbors and number of diseased neighbors. Edge correction was

performed because for a given point, *p*, if all other points within a given distance, *dist*, are considered neighbors, the number of neighboring plants within a circle centered on *p* with a radius of *dist* is smaller if *p* is on or near the edge of the plot than if *p* is in the center of the plot. This is because the circle with radius *dist* encompassing all neighbors when *p* is on the edge extends beyond the plot borders. To adjust for this, plot edge correction calculations were performed using the 27 explicit formulas designed to account for the area external to a rectangular plot outlined by Goreaud and Pélissier (1999). The second modification was made because as the cutoff distance to be considered a neighbor increases, the number of neighbors increase. Including total neighbors and diseased neighbors as a natural log scaled product corrects for this increase in number of plants. The scaling is important to keep the product small so the product and simple count or Cauchy summation is of a similar magnitude and therefore can potentially exhibit an effect on the logistic regression.

For each of the two base models (simple count and Cauchy), two variants of the models were run (unadjusted and adjusted for number of neighbors, each with edge correction) for each of the four crop + year combinations (tomato, pepper, 2006, 2007) for each sample period after TSW was observed within a plot. The values calculated using these models were used as independent variables in stepwise logistic regression analysis. However, only one parameter from any one sample period was permitted to enter the stepwise regression. The sample period and row-space combinations are designated *S#R#* in the regression analysis results. In addition to these parameters, developmental degree days were calculated for each crop through the end of the previous sample period using the transplant

date (Tables 3-6) as the start of degree day accumulation. Lower developmental thresholds of 10°C and 12.8°C were used for tomato and pepper, respectively (Soto-Ortiz and Silvertooth 2008, Flint 1999). In the logistic regression analysis models, this parameter is designated *CropDD#*, where # represents the sample period through which degree days have been accumulated. This parameter was included to account for mature-plant resistance that was expected to affect late season infection of plants.

Results

TSW Data. In both 2006 and 2007, a large range of TSW final prevalence was observed in the tomato and pepper plots (Figure 2). Final TSW prevalence in 2006 tomato plots was as little as 2.1% in Plot 4 and as much as 66.6% in Plot 3A. In 2007, the range was slightly less with 18.6 % in Plot 7B and 45.2 % in Plot 6A. The 2006 pepper plots ranged in final TSW prevalence from 10.2 to 65.4% in Plots 10B and 11B, respectively. The observed range in 2007 pepper plots was greater; Plot 13A had a final prevalence of only 2.3%, but nearly all pepper plants in Plot 14A were diseased (96.3%). Sufficient TSW was observed in each year and each crop that it was plausible to observe secondary spread of TSW.

Thrips Collection Data. Sticky traps internal to plots were collected in 2006 and 2007 to determine whether vector species of thrips were present in tomato and pepper fields. It is apparent from internal trapping data from both years that few *F. fusca* were present in tomato and pepper fields. The greatest average capture of *F. fusca* in either crop was less than three adult individuals per day, and average sticky trap captures were typically two or fewer adults per day (Figs. 3a & c, 4 a & c). In contrast, about two to five times more *F.*

occidentalis than *F. fusca* adults were captured daily from tomato fields in 2006 and 2007 (Figs. 3a-b, 4 a-b). The numbers of average daily *F. occidentalis* captured from pepper fields was variable from plot to plot. In 2006, almost no *F. occidentalis* were captured from Plot 10A, but average daily captures from Plot 8 exceeded 30 *F. occidentalis* adults for one sample period; however, the average daily capture for the sample periods prior to and after this peak capture had ca. seven to 10 times fewer *F. occidentalis* (Figure 3d). In 2007, the numbers of average daily *F. occidentalis* captured from Plot 15A were large, peaking at more than 30 adults per day, but captures were moderate and low from Plots 14A&B and 12A, respectively (Figure 4d).

Repeated measures analysis of thrips captured on sticky traps internal and external to tomato and pepper fields in 2007 showed that the numbers of *F. fusca* captured were statistically smaller from internal traps than external traps for tomato Plot 5 ($p = 0.0003$), pepper Field 14 (Plots A and B combined; $p = 0.0113$), and pepper Plot 15A ($p = 0.0391$; Table 2). The numbers of *F. fusca* captured on internal and external sticky traps from tomato Field 6 (Plots 6A and B; $p = 0.7890$) and pepper Plot 12A ($p = 0.6695$) were not significantly different (Table 2). However, significantly more *F. occidentalis* were captured from internal sticky traps compared to external sticky traps in tomato Field 6 (Plots 6A and B; $p < 0.0001$), Plot 7A ($p = 0.0378$), pepper Field 14 (Plots 14A and B; $p = 0.0113$), and Plot 15A ($p < 0.0001$) (Table 2). No significant difference was observed between internal and external sticky trap captures of *F. occidentalis* for tomato Plot 5 ($p = 0.3325$) or pepper Plot 12A ($p = 0.0765$) (Table 2).

These sticky trap data suggest that *F. occidentalis* become resident in at least some tomato and pepper fields, but evidence does not suggest that *F. fusca* establish populations within either crop. Similar trends are observed in the thrips census data from foliage and blossom samples. Very few immature *F. fusca* were collected from tomato foliage during the 2007 season (Figure 5a). A few adult *F. fusca* were collected from tomato foliage samples in mid-May of 2007; the average capture was less than three adults per 5g dry weight of foliage, but *F. fusca* were nearly absent from subsequent samples (Figure 5b). However, immature *F. occidentalis* were present on tomato foliage throughout the season, initially at low levels (typically less than an average of 10 individuals per 5g dry weight of foliage) in the early season but increasing to ca. 20-60 individuals per 5g sample by mid-June (Figure 5c). The peak immature *F. occidentalis* captures from tomato foliage followed peak adult captures in early June (Figure 5 c-d). Similar to observations from the tomato foliage samples, few adult *F. fusca* were collected from tomato blossoms. Peak adult *F. fusca* captures in late May averaged less than 1.5 individuals per 10 blossoms and the number of individuals collected after the peak remained low (Figure 6a). No immature *F. fusca* were collected from blossom samples. Immature *F. occidentalis* were consistently present in tomato blossom samples throughout the season, though fewer individuals were collected from blossom samples than from foliage samples (Figs. 5c, 6b). Similar to collections from tomato foliage, peak adult *F. occidentalis* collections occurred in late May and early June (Figure 6c); however, about twice as many adult *F. occidentalis* were collected from tomato blossoms than foliage samples during peak sample periods (Figs. 5d, 6c).

From pepper plots, very few immature and adult *F. fusca* were collected from foliage samples (Figure 7a-b). The average number of *F. fusca* collected each sample period for a given plot was less than one individual. Immature and adult *F. occidentalis* were present in pepper foliage samples throughout the season in the majority of plots, but the average number of *F. occidentalis* collected from an individual plot for a given sample period ranged from very low (less than one individual) to very high (more than 10 and 50 immature and adult individuals, respectively) (Figure 7c-d). No immature and very few adult *F. fusca* were collected from pepper blossoms throughout the season (Figure 8a). For a given plot and sample period, the average number of adult *F. fusca* collected from five samples of five blossoms was less than one individual. On average, two or fewer immature *F. occidentalis* individuals were collected from the five blossom samples from each plot on a given sample date, but some individuals were collected on each date for most plots (Figure 8b). In contrast, the number of adult *F. occidentalis* collected was variable, ranging from zero individuals to more than 50 individuals. However, on average, most pepper blossom samples contained one or more adult *F. occidentalis* (Figure 8c).

Transmission Assay. Only seven immature *F. fusca* were collected from tomato foliage and blossoms from infected plants. Of these, two individuals transmitted TSWV to petunia leaf disks as adults (Table 4). Three immature *F. fusca* were collected from all pepper foliage and blossom samples. Of these, only one transmitted TSWV to a petunia leaf disk as an adult (Table 6). The small numbers of *F. fusca* collected from these samples is consistent with trapping data from both tomato and pepper fields.

Across all sample dates and tomato plots, 637 immature *F. occidentalis* were collected from tomato foliage and blossom samples from infected plants, reared to adult, and tested for the ability to transmit TSWV to petunia leaf disks. Data from foliage and blossom samples are not presented separately because it is possible that thrips hatched from one area of the plant and travelled to another area of the plant. However, immature thrips mobility is limited enough that they are likely to remain on the plant from which they hatched while developing as first and second instars. Although the location from which an individual *F. occidentalis* hatched is unknown, individuals collected from both foliage and blossoms transmitted TSWV. Of the *F. occidentalis* collected from tomato plants, 46 individuals (7.2%) transmitted TSWV to petunia leaf disks (Table 4). Over the entire season, the total percentage of *F. occidentalis* that transmitted TSWV to petunia leaf disks ranged from 4.4-10.5% across plots (Table 4).

Overall, 54 of 261 (20.7%) *F. occidentalis* collected as immature thrips from infected pepper plants transmitted TSWV to petunia leaf disks as adults (Table 6). By plot, the percentage of transmitting *F. occidentalis* across the entire season ranged from 0 to 29.6, but for sample period six, the range of transmission was 0-41.0%.

Adult Generation Turnover Dates. Sufficient developmental time passed between initial TSW infections and harvest for potential secondary spread by *F. fusca* and *F. occidentalis* that hatch on infected tomato and plants (Tables 3-6). In tomato fields, sufficient degree days were accumulated so that up to four generations of *F. fusca* adults and five generations of *F. occidentalis* adults may have developed from initial vectors that

immigrated into the fields and oviposited eggs on infected plants. The exact number of generations able to develop based on degree day calculation for each tomato are presented in Tables 3-4. Degree day accumulation for the pepper fields was sufficient for up to four generations of *F. fusca* and *F. occidentalis* to become adults. Specific number of generations able to develop in pepper plots are presented in Tables 5-6. Although TSW symptoms may take one to several weeks post infection to be expressed, sufficient time (4-8 weeks) passed for at least the F1, and commonly F2 progeny to infect non-diseased plants as adults and for the infected plants to become symptomatic prior to the end of the season. Depending on the plot, additional generations of thrips vectors would have had sufficient developmental time to contribute to secondary spread of TSWV. In some plots (ex. 7A, 15B), sufficient developmental time passed between primary TSW infection and the end of the season to potentially observe secondary spread from F3 and F4 generations of adults. Developmental time was not a constraint to secondary spread of TSWV in the observed tomato and pepper fields.

Secondary Spread Models. Based on the adult generation turnover dates calculated and the time that typically passes from TSWV infection to symptom expression, observable patterns of secondary spread were expected late season (sample periods 5-7). The best overall model for each late season sample period (sample periods 5-7) are presented in Tables 7-10. The criteria for choosing the best model was the edge corrected model base type with or without modification to account for the proportion of plants infected with the largest model chi-square value (likelihood ratio) in the majority of sample periods. For tomato fields, the

Cauchy model was selected (Tables 7-8). For pepper fields, the count model was selected (Tables 9-10). Logistic regression models for 2006 tomato plots that relate whether or not an asymptomatic plant will become symptomatic to presence of diseased neighbors contain parameters of diseased neighbor parameters within one row space in regression models for sample periods six and seven indicating that very close neighbors are important to whether or not a susceptible plant will become infected (Table 7). Models for sample periods five and six include parameters incorporating neighbor data from seven and nine row spaces, respectively, indicating that plants relatively far away (ca. 6 – 13 m) are important in predicting whether or not a susceptible plant will become diseased. The model for the 2007 tomato fields during sample period six contained a parameter indicating that diseased plants within one row space is important to explain observed infection. However, models for sample periods five and six do not contain model parameters indicating that plants within a short distance (1-3 row spaces) are important to explaining observed infection. *CropDD* was never selected as a model parameter for 2006 or 2007 tomato models.

Pepper plot models for 2006 and 2007 use the count base parameter calculation and do not include any neighbor parameters associated with one, two or three row spaces (Tables 9-10). *CropDD* was included in the 2006 sample period five and 2007 sample periods five and six models (Tables 9-10). The coefficient of *CropDD* is negative in two cases possibly indicating that as the crop matures (*CropDD* increases), a susceptible plant is less likely to become infected.

Discussion

Previous work based on TSW disease observations indicated that secondary spread of TSWV either did not occur or was of limited importance in tomato and pepper (Gitaitis et al. 1998). However, personal observations of tomato and pepper fields with high TSW prevalence at the end of the growing season with limited surrounding weed hosts provided some indicaiton that hosts external to the fields may not be the only source of TSWV. In addition, some insecticide programs have been shown to reduce late season increases in TSW symptomatic tomato plants (Riley and Pappu 2000). Based on the data collected for this study, the potential for secondary spread exists in both tomato and pepper. Competent vector thrips are present, sufficient developmental time passes for transmission of TSWV and disease expression to occur, and, at least in tomato fields, the presence of diseased nearby neighbor plants is important to whether or not a susceptible plant will become infected. Models did not indicate evidence of secondary spread in pepper, but based on competent vector presence, the potential exists.

Sticky trap, foliage, and blossom data indicate that *F. fusca* are transient and do not establish resident populations within tomato and pepper fields, but *F. occidentalis* does colonize at least some fields of both crops. Based on the thrips foliage and blossom census samples, when *F. occidentalis* are present within a tomato field, the number of immature *F. occidentalis* from five grams (dry weight) of tomato foliage ranges from about three to 30 for an average of ten samples. Assuming a tomato plant consists of at least 100 g (dry weight) of foliage and three immature *F. occidentalis* are present per 5 g, one might expect 60 immature

F. occidentalis on the foliage on a given sample date. The overall percentage of *F. occidentalis* collected from infected plants that transmitted TSWV is 7.2%. This equates to ca. 4.3 infected competent TSWV vectors per 100g (dry weight) of tomato foliage. Often, 10 immature *F. occidentalis* were collected from the 5g sample. This would potentially lead to 41.1 TSWV vectors developing on an infected plant on a given sample date. If the *F. occidentalis* were at observed peak levels (ca. 30 thrips per average of 10 foliage samples), it is conceivable that a 100g (dry weight) plant could host 43.2 infected thrips on a given sample date.

The number of immature *F. occidentalis* collected from 5g dry weight of pepper foliage ranged from about three to ten individuals on average for a given sample date and transmission studies yielded an overall estimate of 20.7% of *F. occidentalis* collected as immature thrips as competent vectors. Assuming a pepper plant consists of 100 g (dry weight) of foliage, one might expect 60 to 200 immature *F. occidentalis* present developing on an infected plant on a particular sample date. If 20.7% of the thrips become viable vectors, 12.4 to 41.4 *F. occidentalis* individuals per diseased plant per sample period may be present and able to contribute to secondary spread of TSWV as adults. These estimates of potential viruliferous thrips progeny from tomato and pepper plants do not account for factors such as density dependent changes in oviposition behavior that may limit the number of thrips eggs per plant, but they do illustrate that a large number of thrips capable of spreading TSWV might be produced on a single infected plant.

It was expected that parameters using neighbors within one, two, or three row spaces would be chosen in stepwise regression models if secondary spread by *F. occidentalis* occurs because *F. occidentalis* have been documented as moving short distances among host plants (Groves et al. 2001). However, since it was not possible to track individual thrips movement in this study, the actual distance of *F. occidentalis* movement is unknown. Evidence of late season secondary spread in tomato is supported, but models do not indicate that nearby plants (within 1-3 row spaces) are important in explaining the overall pattern of disease in pepper. However, some of the assumptions inherent in expected patterns of secondary disease spread could be false for this system:

1. TSW patterns may not track thrips dispersal patterns. Use of an insect dispersal model to describe an insect-transmitted disease inherently assumes that the insect vectors transmit TSWV equally well at all distances travelled from an initial infected host plant. Thrips vectors do not transmit each time they feed (Rotenberg et al. 2009, Wijkamp and Peters 1993) and feeding duration may not be constant with distance travelled; therefore, some plants to which thrips vectors have dispersed may not become infected. Also, mature plant resistance has been documented in pepper. Susceptibility to TSWV decreases by 50% within three to nine days post transplant assuming plants are 42 days old at transplant (Beaudoin et al. 2009). Therefore, it is likely that a larger percentage of feeding by thrips causes TSWV infection in the early season compared to the late season for a given thrips pressure. Because of the increased difficulty to infect a plant with age, it is possible that a thrips will successfully transmit TSWV less frequently to older plants, and therefore, the

distance a thrips travels on average before infecting a plant may increase as the season progresses, causing the relationship between thrips movement and TSW expression to change over time.

2. TSW symptoms that appear during the same sample period do not necessarily reflect infection that occurred at the same time. The lag time of TSW symptom development after initial infection with TSWV varies by plant. Symptom expression of TSWV infection can begin in as little as a week or after more than a month post initial infection. If time from infection to symptom expression was highly variable within the study plots, it is possible that secondary spread patterns are not detectable because date of symptom expression, not date of infection was recorded. It is possible that TSW could have replicated and spread throughout a plant prior to the observation of disease and thrips vectors could potentially contribute to secondary spread if they hatched on an asymptomatic TSWV-infected plant.

3. Multiple vector species may have different dispersal patterns and therefore create two separate patterns of TSW disease spread that, when overlaid on one another, obscure one or both patterns. Data from this study and Chapter 3 indicate that *F. fusca* are transient vectors that do not establish populations within tomato or pepper fields and that individuals are capable of flying hundreds of meters across a field. In contrast, *F. occidentalis* establish resident populations within tomato and pepper fields and typically disperse short distances compared to *F. fusca* (Groves et al. 2001).

4. If primary spread occurs continuously throughout the season, the patterns of primary and secondary TSW spread may obscure each other. It is possible that short-distance

dispersing, resident *F. occidentalis* cause late season secondary spread of TSWV in tomato and pepper fields, but *F. fusca* may disperse hundreds of meters, originating from hosts external to the field, and transmit TSWV randomly throughout the field. If *F. fusca* transmit TSW to plants continuously throughout the growing season, it could obscure a subtle, clustering effect of *F. occidentalis* secondary spread.

5. It is possible that patterns of secondary spread are not detectable due to the plot sizes used in these studies. If TSW in an entire tomato or pepper field was observed periodically for the duration of an experiment, it is possible that patterns of TSW would be observed since spatial patterns are dependent on observation at an appropriate scale. Pepper plot dimensions were 8.1 x 15.3 m, 10.7 x 19.1 m, and 15.2 x 15.3 m. Thrips vectors originating from within a pepper field may travel distances that are longer than the plot dimensions studied. In this case, a larger plot size would be required to detect secondary spread patterns.

6. Expected patterns of secondary spread such as diseased neighbor effects assume that thrips vectors that contribute to secondary TSWV spread move and transmit TSW from origin points to susceptible plants that are relatively close, but this might not be true. One could assume that if vectors move long distances throughout the field, vectors would exit the field. However, field margin cues such as the reflective contrast of a field edge and soil (Prokopy and Owens 1983) or even a field edge and weedy margin could serve as a visual barrier that thrips vectors choose not to cross. Ability to move across an entire field but a preference to remain within a field could cause a random pattern of TSW because the ability

to move exceeds the field dimensions. Thrips could travel anywhere within a field and transmit TSW. *F. fusca* are able to disperse long distances across a field, but do not establish resident populations within tomato and pepper fields, and *F. occidentalis* have been observed to disperse short distances within weed hosts, so data observed in this study do not support this possibility of why secondary spread was not observed. However, it is important to be mindful when considering secondary spread within any system that expected disease patterns are influenced by insect choices as well as physical limitations of ability.

Although, conclusive evidence of secondary spread by *F. occidentalis* in pepper fields was not found utilizing regression model analysis, an anecdotal observation further substantiates that secondary spread may occur but not be apparent in patterns of disease within the field. Adjacent to pepper Field 15 was a several acre tobacco field. Surrounding the pepper and tobacco fields were small weedy margins, grass, and a melon plot. Observed final TSW prevalence for Field 15 was over 90%, while the final TSW prevalence in the adjacent tobacco field was 4% based on visual scoring of several hundred plants. The difference in average number of adult *F. occidentalis* captured per day on internal versus external sticky traps was 0.6, 1.9, 11.5, 28.6, and 22.3 individuals on sample dates 1-5 (Figure 4d). The large number of *F. occidentalis* captured on internal compared to external sticky traps from mid to late season and the dramatically different final prevalence percentages of TSW in each field could plausibly be explained by secondary spread of TSW within the pepper field. It is unlikely to be a simple matter of host preference of pepper over tobacco by *F. occidentalis* originating from weeds because the number of *F. occidentalis*

captured on traps external to the pepper field were low for the duration of the experiment. Overall, the data collected indicate that secondary spread of TSW within tomato and pepper fields by *F. occidentalis* is possible and likely in tomato fields and pepper Field 15, though confirmation via TSW disease patterns was not established for pepper.

References Cited

Atiri, G. I., D. A. Enobakhare, and G. Thottappilly. 1986. The importance of colonizing and non-colonizing aphid vectors in the spread of cowpea aphid-borne mosaic virus in cowpea. Crop Prot. 5: 406-410.

Beaudoin, A. L. P., N. D. Kahn, and G. G. Kennedy. 2009. Bell and banana pepper exhibit mature-plant resistance to tomato spotted wilt tospovirus transmitted by *Frankliniella fusca* (Thripidae: Thysanoptera). J. Econ. Entomol. 102: 30-35.

Chancellor, T. C. B., A. G. Cook, and K. L. Heong. 1996. The within-field dynamics of rice tungro disease in relation to the abundance of its major leafhopper vectors. Crop Prot. 15: 439-449.

Coutts, B.A., M.L. Thomas-Carroll, and R.A.C. Jones. 2004. Patterns of spread of tomato spotted wilt virus in field crops of lettuce and pepper: spatial dynamics and validation of control measures. *Annals of Applied Biology.* 145: 231-245.

Eckel, C. S., K. Cho, J. F. Walgenbach, G. G. Kennedy, and J. W. Moyer. 1996. Variation in thrips species composition in field crops and implications for tomato spotted wilt epidemiology in North Carolina. Entomol. Exp. Appl. 78: 19-29.

Flint, M. L. (ed.) 1999. Growth and development of tomatoes. pp. 8-13. *In* Integrated pest management for tomatoes, 4th ed. A N R Publications, Richmond, CA.

Gitaitis, R. D., C. C. Dowler, and R. B. Chalfant. 1998. Epidemiology of tomato spotted wilt in pepper and tomato in southern Georgia. Plant Dis. 83: 752-756.

Goreaud, F. and R. Pélissier. 1999. On explicit formulas of edge effect correction for Ripley's K-function. J. Vegetation Sci. 10: 433-438.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2001. Overwintering of *Frankliniella fusca* (Thysanoptera: Thripidae) on winter annual weeds infested with tomato spotted wilt virus and patterns of virus movement between susceptible hosts. *Phytopathol.* 91: 891-899.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2003. Seasonal dispersal patterns of *Frankliniella fusca* (Thysanoptera: Thripidae) and tomato spotted wilt virus occurrence in central and eastern North Carolina. J. Econ. Entomol. 96: 1-11.

Higley, L. G., L. P. Pedigo, and K. R. Ostlie. 1986. DEGDAY: a program for calculating degree-days, and assumptions behind the degree-day approach. Environ. Entomol. 15: 999-1016.

Linford, M. B. 1962. Transmission of the pineapple yellow-spot virus by *Thrips tabaci*, pp. 301-324. *In* K. Maramorosch (ed.) Biological transmission of disease agents: symposium held under the auspices of the Entomological Society of America: Atlantic City, 1960. Academic Press, New York.

Lowry, V. K., J. W. Smith, and F. L. Mitchell. 1992. Life-fertility tables for *Frankliniella fusca* (Hinds) and *F. occidentalis* (Pergande) (Thysanoptera: Thripidae) on peanut. Ann. Entomol. Soc. Am. 85: 744-754.

Mayer, D. G. and M. G. Atzeni. 1993. Estimation of dispersal distances for *Cochliomyia homnivorax* (Diptera: Calliphoridae). Environ. Entmol. 22: 368-374.

Morsello, S. C., A. L. P. Beaudoin, R. L. Groves, B. A. Nault, and G. G. Kennedy. 2010. The influence of temperature and precipitation on spring dispersal of *Frankliniella fusca* changes as the season progresses. Entomol. Exp.Appl. 134: 260-271.

Palmer, J. M., L. A. Mound, and G. J. du Haeume. 1992. IIE guides to insects of importance to man, vol. 2. Thysanoptera (ed. by CR Betts), pp. 73. International Institute of Entomology, CAB International, Wallingford, UK.

Prokopy, R.J. and E.D. Owens 1983. Visual detection of plants by herbivorous insects. Ann. Rev. Entomol. 28: 337-364.

Riley, D. G. and H. R. Pappu. 2000. Evaluation of tactics for management of thrips-vectored *Tomato spotted wilt virus* in tomato. Plant Dis. 84: 847-852.

Rotenberg, D. N., K. K. Kumar, D. E. Ullman, M. Montero-Astúa, D. K Willis, T. L. German, and A. E. Whitfield. 2009. Variation in *tomato spotted wilt virus* titer in *Frankliniella occidentalis* and its association with frequency of transmission. Phytopathol. 99: 404-410.

Sakimura, K. 1962. The present status of thrips-borne viruses, pp. 33-40. *In* K. Maramorosch (ed.) Biological transmission of disease agents: symposium held under the auspices of the Entomological Society of America: Atlantic City, 1960. Academic Press, New York.

SAS Institute, Inc. 2005. SAS® 9.1.3 Intelligence Platform: Single-User Installation Guide. Cary, North Carolina, USA.

Soto-Ortiz, R. and J. C. Silvertooth. 2008. A crop phenology model for irrigated New Mexico chile (*Capsicum annuum* L.) type varieties. Vegetable Report. P-152, p. 104-112.

van de Wetering, F., R. Goldbach, and D. Peters. 1996. Tomato spotted wilt tospovirus ingestion by first instar larvae of *Frankliniella occidentalis* is a prerequisite for transmission. Phytopathol. 86(9): 900-905.

Whitfield, A.E., D.E. Ullman, and T.L. German. 2005. Tospovirus-thrips interactions. Annu. Rev. Phytopathol. 43: 459-489.

Wijkamp, I. and D. Peters. 1993. Determination of the median latent period of two tospoviruses in *Frankliniella occidentalis*, using a novel leaf disk assay. Phytopathol. 83: 986-991.

Table 1. Summary of plot characteristics, field number and plot letter designations, and samples collected.

Crop	Type	Variety	Year	Plot #	# of Rows Sampled	Row Type	Row Spacing (m)	Plant Spacing (m)	Plant Stand Count[1]	First Sample Date	# Plants Infected on First Sample Date	Ground Cover	Internal Traps	External Traps	PLDA[2] Samples
Tomato	Grape	Smartie	2006	1	10	Single Bedded	1.524	0.610	500	5/30/2006	2	Black Mulch	Yes	No	No
	Grape	Cupid	2006	2	10	Single Bedded	1.524	0.610	500	5/30/2006	0	Black Mulch	Yes	No	No
	Grape	Smartie	2006	3A	10	Single Bedded	1.524	0.610	500	5/30/2006	4	Black Mulch	Yes	No	No
	Grape	Smartie	2006	3B	10	Single Bedded	1.524	0.610	500	5/30/2006	9	Black Mulch	No	No	No
	Fresh Market	Unknown	2006	4	6	Single Bedded	1.524	0.610	990	5/19/2006	0	Black Mulch	No	No	No
	Grape	Cupid	2007	5	10	Single Bedded	1.524	0.610	493	4/24/2007	0	Black Mulch	Yes	Yes	Yes
	Grape	Cupid	2007	6A	10	Single Bedded	1.524	0.610	493	4/24/2007	0	Black Mulch	Yes	Yes	Yes
	Grape	Cupid	2007	6B	10	Single Bedded	1.524	0.610	499	4/24/2007	0	Black Mulch	Yes	Yes	Yes
	Grape	Cupid	2007	7A	10	Single Bedded	1.524	0.610	496	4/24/2007	0	Black Mulch	Yes	Yes	Yes
	Grape	Cupid	2007	7B	10	Single Bedded	1.524	0.610	499	4/24/2007	0	Black Mulch	No	Yes	Yes
Pepper	Sweet Bell	Unknown	2006	8A	10	Single Bedded	0.813	0.305	500	5/19/2006	1	Bare Soil	Yes	No	No
	Sweet Bell	Unknown	2006	8B	10	Single Bedded	0.813	0.305	500	5/19/2006	1	Bare Soil	No	No	No
	Sweet Bell	Unknown	2006	9A	10	Single Bedded	0.813	0.305	500	5/19/2006	0	Bare Soil	No	No	No
	Sweet Bell	Unknown	2006	9B	10	Single Bedded	0.813	0.305	500	5/19/2006	0	Bare Soil	No	No	No
	Sweet Bell	Unknown	2006	10A	10	Single Bedded	0.813	0.305	500	5/30/2006	7	Bare Soil	Yes	No	No
	Sweet Bell	Unknown	2006	10B	10	Single Bedded	0.813	0.305	500	5/30/2006	12	Bare Soil	No	No	No
	Sweet Bell	Unknown	2006	11A	10	Single Bedded	1.067	0.381	500	5/30/2006	6	Bare Soil	Yes	No	No
	Sweet Bell	Unknown	2006	11B	10	Single Bedded	1.067	0.381	500	5/30/2006	11	Bare Soil	No	No	No
	Sweet Bell	Revolution	2007	12A	10	Double Bedded	1.524	0.305	992	5/1/2007	1	Black Mulch	Yes	Yes	Yes
	Sweet Bell	Revolution	2007	12B	10	Double Bedded	1.524	0.305	994	5/1/2007	1	Black Mulch	No	Yes	Yes
	Sweet Bell	Revolution	2007	13A	10	Double Bedded	1.524	0.305	995	5/1/2007	0	Black Mulch	No	No	Yes
	Sweet Bell	Revolution	2007	13B	10	Double Bedded	1.524	0.305	995	5/1/2007	0	Black Mulch	No	No	Yes
	Sweet Bell	Alliance	2007	14A	10	Single Bedded	1.067	0.381	487	5/1/2007	0	Bare Soil	Yes	Yes	Yes
	Sweet Bell	Alliance	2007	14B	10	Single Bedded	1.067	0.381	481	5/1/2007	0	Bare Soil	Yes	Yes	Yes
	Banana	Allara	2007	15A	10	Single Bedded	0.813	0.305	499	5/2/2007	0	Bare Soil	Yes	Yes	Yes
	Banana	Allara	2007	15B	10	Single Bedded	0.813	0.305	494	5/2/2007	0	Bare Soil	No	Yes	Yes

[1] In 2006, plant stand counts were made on the first sample period when plots were set up. In 2007, plant stand counts were the number of live plants within the boundaries of a given plot on the first sample date when TSW was first observed in the plot. Plant stand count was used as the total number of plants within a plot when calculating the percentage of plants with TSW. [2] PLDA = Petunia leaf disk assay performed using immature thrips collected from plots and reared to adults to test for TSWV transmission.

Table 2. Contrasts comparing thrips captures on internal and external sticky traps.

Statistically significant contrasts are in bold.

Crop	Plot	Thrips species	Interior Mean	Exterior Mean	df	F-value	P-value
Tomato	**5**	***F. fusca***	**0.68 (0.93)**	**3.50 (6.40)**	**1, 67**	**14.73**	**0.0003**
Tomato	6A-B	*F. fusca*	0.76 (1.11)	0.79 (1.13)	1, 143	0.08	0.7809
Tomato	7A	*F. fusca*	0.71 (0.92)	0.78 (1.32)	1, 68	0.13	0.7232
Tomato	5	*F. occidentalis*	9.69 (6.24)	13.26 (10.52)	1, 67	0.95	0.3325
Tomato	**6A-B**	***F. occidentalis***	**11.53 (5.86)**	**4.02 (5.09)**	**1, 143**	**25.08**	**< 0.0001**
Tomato	**7A**	***F. occidentalis***	**8.52 (5.35)**	**5.59 (5.30)**	**1, 68**	**4.49**	**0.0378**
Pepper	12A	*F. fusca*	1.10 (1.00)	1.02 (0.85)	1, 68	0.18	0.6695
Pepper	**14A-B**	***F. fusca***	**0.84 (0.89)**	**1.45 (1.69)**	**1, 85**	**6.71**	**0.0113**
Pepper	**15A**	***F. fusca***	**1.79 (1.46)**	**2.61 (2.27)**	**1, 52**	**4.48**	**0.0391**
Pepper	12A	*F. occidentalis*	2.69 (3.91)	1.39 (1.22)	1, 68	3.24	0.0765
Pepper	**14A-B**	***F. occidentalis***	**6.69 (9.48)**	**1.02 (1.61)**	**1, 85**	**12.57**	**0.0006**
Pepper	**15A**	***F. occidentalis***	**16.47 (11.93)**	**5.34 (1.78)**	**1, 52**	**44.61**	**< 0.0001**

Table 3. Expected generations of adult thrips present on each sample date in 2006 tomato plots. Dates on which thrips were expected to become adults and potentially contribute to secondary spread of TSW are indicated in parentheses following the generation designation.

Plot	Event	Date	Current Adult Generation[1]	
			F. fusca	*F. occidentalis*
1, 3A, 3B	Transplant[2]	4/15/2006	-	-
	Sample 1	-	-	-
	Sample 2	-	-	-
	Sample 3	**5/30/2006**	F0	F0
	Sample 4	6/13/2006	F1 (6/11/2006)	F1 (6/7/2006)
	Sample 5	6/27/2006	F1	F2 (6/23/2006)
	Sample 6	7/11/2006	F2 (6/28/2006)	F3 (7/5/2006)
	Sample 7	7/26/2006	F3 (7/14/2006)	F4 (7/19/2006)
2	Transplant	4/15/2006	-	-
	Sample 1	-	-	-
	Sample 2	-	-	-
	Sample 3	5/30/2006	-	-
	Sample 4	**6/13/2006**	F0	F0
	Sample 5	6/27/2006	F1 (6/24/2006)	F1 (6/21/2006)
	Sample 6	7/11/2006	F2 (7/10/2006)	F2 (7/4/2006)
	Sample 7	7/26/2006	-	-
4	Transplant	4/15/2006	-	-
	Sample 1	-	-	-
	Sample 2	-	-	-
	Sample 3	**5/19/2006**	F0	F0
	Sample 4	6/13/2006	F1 (6/3/2006)	F1 (5/31/2006)
	Sample 5	6/27/2006	F2 (6/23/2006)	F2 (6/16/2006)
	Sample 6	7/11/2006	F3 (7/9/2006)	F3 (6/29/2006)
	Sample 7	7/26/2006	F4 (7/23/2006)	F4 (7/13/2006), F5 (7/25/2006)

[1] Generation turnover dates were calculated using the half-sine degree day model with degree day accumulation beginning one week prior to the first observation of TSW within a given plot (TSW symptom expression typically occurs one or more weeks after initial infection). The first sample date on which TSW was observed within a given plot is indicated in bold. [2] Exact transplant dates are unknown and are assumed to be 4/15/2006.

Table 4. Expected generations of adult thrips vectors present on each sample date and results from immature thrips transmission assays from 2007 tomato plots. Dates on which thrips were expected to become adults and potentially contribute to secondary spread of TSW are indicated in parentheses following the generation designation.

			Current Adult Generation[1]		% PLDA[2] disks positive	
Plot	**Event**	**Date**	***F. fusca***	***F. occidentalis***	***F. fusca***	***F. occidentalis***
5	Transplant	4/17/2007	-	-	-	-
	Sample 1	4/24/2007	-	-	-	-
	Sample 2	5/8/2007	-	-	NT	NT
	Sample 3	**5/22/2007**	F0	F0	NT	0 (n = 6)
	Sample 4	6/6/2007	F1 (6/5/2007)	F1 (6/1/2007)	NT	5.2 (n=19)
	Sample 5	6/20/2007	F1	F2 (6/16/2007)	0 (n=1)	3.7 (n=27)
	Sample 6	7/5/2007	F2 (6/23/2007)	F3 (6/30/2007)	NT	5.8 (n=52)
	Sample 7	7/18/2007	F3 (7/8/2007)	F4 (7/13/2007)	NT	21.4 (n=28)
					Total 0 (n=1)	Total 8.3 (n=132)
6A	Transplant	4/10/2007	-	-	-	-
	Sample 1	4/24/2007	-	-	-	-
	Sample 2	5/8/2007	-	-	NT	NT
	Sample 3	**5/22/2007**	F0	F0	0 (n=2)	7.8 (n=13)
	Sample 4	6/6/2007	F1 (6/5/2007)	F1 (6/1/2007)	NT	0 (n=13)
	Sample 5	6/20/2007	F1	F2 (6/16/2007)	NT	18.2 (n=11)
	Sample 6	7/5/2007	F2 (6/23/2007)	F3 (6/30/2007)	NT	2.2 (n=46)
	Sample 7	7/18/2007	F3 (7/8/2007)	F4 (7/13/2007)	NT	8 (n=25)
					Total 0 (n=2)	Total 5.6 (N=108)
6B	Transplant	4/10/2007	-	-	-	-
	Sample 1	4/24/2007	-	-	-	-
	Sample 2	5/8/2007	-	-	NT	NT
	Sample 3	**5/22/2007**	F0	F0	NT	0 (n=4)
	Sample 4	6/6/2007	F1 (6/5/2007)	F1 (6/1/2007)	NT	0 (n=12)
	Sample 5	6/20/2007	F1	F2 (6/16/2007)	0 (n=1)	2.3 (n=37)
	Sample 6	7/5/2007	F2 (6/23/2007)	F3 (6/30/2007)	NT	1.8 (n=56)
	Sample 7	7/18/2007	F3 (7/8/2007)	F4 (7/13/2007)	1 (n=1)	17.6 (n=51)
					Total 50 (n=2)	Total 6.9 (N=160)
7A	Transplant	4/10/2007	-	-	-	-
	Sample 1	4/24/2007	-	-	-	-
	Sample 2	**5/8/2007**	F0	F0	NT	NT
	Sample 3	5/22/2007	F1 (5/27/2007)	F1 (5/21/2007)	NT	0 (n=5)
	Sample 4	6/6/2007	F2 (6/3/2007)	F2 (6/6/2007)	NT	4.5 (n=22)
	Sample 5	6/20/2007	F2	F2	NT	11.1 (n=9)
	Sample 6	7/5/2007	F3 (6/30/2007)	F3 (6/21/2007), F4 (7/4/2007)	NT	5.0 (n=40)
	Sample 7	7/18/2007	F4 (7/15/2007)	F5 (7/17/2007)	NT	18.8 (n=48)
						Total 10.5 (N=124)
7B	Transplant	4/10/2007	-	-	-	-
	Sample 1	4/24/2007	-	-	-	-
	Sample 2	**5/8/2007**	F0	F0	NT	NT
	Sample 3	5/22/2007	F0	F0	NT	0 (n=2)
	Sample 4	6/6/2007	F1 (6/1/2007)	F1 (5/27/2007)	NT	0 (n=14)
	Sample 5	6/20/2007	F2 (6/18/2007)	F2 (6/10/2007)	0 (n=1)	3.0 (n=33)
	Sample 6	7/5/2007	F3 (7/5/2007)	F3 (6/25/2007)	NT	2.3 (n=43)
	Sample 7	7/18/2007	F3	F4 (7/9/2007)	1 (n=1)	14.3 (n=21)
					Total 50 (n=2)	Total 4.4 (N=113)

[1] Generation turnover dates were calculated using the half-sine degree day model with degree day accumulation beginning one week prior to the first observation of TSW within a given plot (TSW symptom expression typically occurs one or more weeks after initial infection). The first sample date on which TSW was observed within a given plot is indicated in bold. [2] PLDA = Petunia leaf disk assay. This assay was performed using thrips collected from plots as immature insects and reared to adults prior to testing for transmission of TSWV. Each thrips was placed on a separate leaf disk. NT indicates that no immature thrips were collected from foliage or blossom samples. Total indicates the overall percentage of all thrips that transmitted out of the total (N) number of thrips collected during the season.

Table 5. Expected generations of adult thrips present on each sample date in 2006 pepper plots. Dates on which thrips were expected to become adults and potentially contribute to secondary spread of TSW are indicated in parentheses following the generation designation.

Plot	Event	Date	Current Adult Generation[1]	
			F. fusca	***F. occidentalis***
8A, 8B	Transplant[2]	4/15/2006	-	-
11A, 11B	Sample 1	-	-	-
	Sample 2	-	-	-
	Sample 3	**5/19/2006**	F0	F0
	Sample 4	6/6/2006	F1 (6/3/2006)	F1 (5/30/2006)
	Sample 5	6/20/2006	F1	F2 (6/15/2006)
	Sample 6	7/5/2006	F2 (6/22/2006)	F3 (6/29/2006)
	Sample 7	7/18/2006	F3 (7/7/2006)	F4 (7/12/2006)
9A, 9B	Transplant	4/15/2006	-	-
	Sample 1	-	-	-
	Sample 2	-	-	-
	Sample 3	5/19/2006	-	-
	Sample 4	6/6/2006	-	-
	Sample 5	**6/20/2006**	F0	F0
	Sample 6	7/5/2006	F1 (6/29/2006)	F1 (6/27/2006)
	Sample 7	7/18/2006	F2 (7/15/2006)	F2 (7/10/2006)
10A, 10B	Transplant	4/15/2006	-	-
	Sample 1	-	-	-
	Sample 2	-	-	-
	Sample 3	**5/30/2006**	F0	F0
	Sample 4	6/6/2006	F0	F0
	Sample 5	6/20/2006	F1 (6/11/2006)	F1 (6/7/2006)
	Sample 6	7/5/2006	F2 (6/28/2006)	F2 (6/23/2006), F3 (7/5/2006)
	Sample 7	7/18/2006	F3 (7/14/2006)	F3

[1] Generation turnover dates were calculated using the half-sine degree day model with degree day accumulation beginning one week prior to the first observation of TSW within a given plot (TSW symptom expression typically occurs one or more weeks after initial infection). The first sample date on which TSW was observed within a given plot is indicated in bold. [2] Exact transplant dates are unknown and are assumed to be 4/15/2006.

Table 6. Expected generations of adult thrips vectors present on each sample date and results from immature thrips transmission assays from 2007 pepper plots. Dates on which thrips were expected to become adults and potentially contribute to secondary spread of TSW are indicated in parentheses following the generation code.

Plot	Event	Date	Current Adult Generation[1]		% PLDA[2] disks positive	
			F. fusca	*F. occidentalis*	*F. fusca*	*F. occidentalis*
12A	Transplant	4/10/2007	-	-	-	-
	Sample 1	5/1/2007	F0	F0	-	-
	Sample 2	5/15/2007	F0	F1 (5/12/2007)	NT	10 (n=10)
	Sample 3	5/30/2007	F1 (5/19/2007)	F1	NT	0 (n=13)
	Sample 4	6/13/2007	F2 (6/8/2007)	F2 (5/31/2007)	NT	0 (n=20)
	Sample 5	6/27/2007	F3 (6/25/2007)	F3 (6/11/2007)	0 (n=1)	NT
	Sample 6	7/11/2007	F4 (7/10/2007)	F4 (6/28/2007)	NT	NT
	Sample 7	-	-	-	-	-
					Total 0 (n=1)	Total 2.3 (n=43)
12B	Transplant	4/10/2007	-	-	-	-
	Sample 1	5/1/2007	F0	F0	-	-
	Sample 2	5/15/2007	F0	F1 (5/12/2007)	NT	NT
	Sample 3	5/30/2007	F1 (5/19/2007)	F1	NT	NT
	Sample 4	6/13/2007	F2 (6/8/2007)	F2 (5/31/2007)	NT	25.0 (n=12)
	Sample 5	6/27/2007	F3 (6/25/2007)	F3 (6/11/2007)	NT	0 (n=4)
	Sample 6	7/11/2007	F4 (7/10/2007)	F4 (6/28/2007)	NT	NT
	Sample 7	-	-	-	-	-
						Total 18.8 (n=16)
13A	Transplant	4/17/2007	-	-	-	-
	Sample 1	5/1/2007	-	-	-	-
	Sample 2	5/15/2007	-	-	NT	NT
	Sample 3	5/30/2007	F0	F0	NT	NT
	Sample 4	6/13/2007	F1 (6/10/2007)	F1 (6/7/2007)	NT	0 (n=4)
	Sample 5	6/27/2007	F2 (6/27/2007)	F2 (6/22/2007)	NT	0 (n=5)
	Sample 6	7/11/2007	F2	F3 (7/6/2007)	NT	NT
	Sample 7	-	-	-	-	-
						Total 0 (n=9)
13B	Transplant	4/17/2007	-	-	-	-
	Sample 1	5/1/2007	-	-	-	-
	Sample 2	5/15/2007	F0	F0	NT	-
	Sample 3	5/30/2007	F0	F0	NT	-
	Sample 4	6/13/2007	F1 (6/5/2007)	F1 (6/1/2007)	NT	16.7 (n=6)
	Sample 5	6/27/2007	F2 (6/23/2007)	F2 (6/17/2007)	NT	14.3 (n=14)
	Sample 6	7/11/2007	F3 (7/8/2007)	F3 (6/30/2007)	NT	0 (n=1)
	Sample 7	-	-	-	-	-
					-	Total 14.3 (n=21)

Plot	Event	Date	Current Adult Generation[1]		% PLDA[2] disks positive	
			F. fusca	*F. occidentalis*	*F. fusca*	*F. occidentalis*
14A	Transplant*	4/15/2007	-	-	-	-
	Sample 1	5/1/2007	-	-	-	-
	Sample 2	5/15/2007	F0	F0	NT	37.5 (n=8)
	Sample 3	5/30/2007	F0	F1 (5/27/2007)	NT	0 (n=1)
	Sample 4	6/13/2007	F1 (6/1/2007)	F2 (6/10/2007)	NT	0 (n=4)
	Sample 5	6/27/2007	F2 (6/18/2007)	F3 (6/25/2007)	NT	0 (n=4)
	Sample 6	7/11/2007	F3 (7/5/2007)	F4 (7/9/2007)	NT	NT
	Sample 7	-	-	-	-	-
						Total 17.6 (n=17)
14B	Transplant*	4/15/2007	-	-	-	-
	Sample 1	5/1/2007	-	-	-	-
	Sample 2	5/15/2007	F0	F0	NT	22.2 (n=27)
	Sample 3	5/30/2007	F0	F1 (5/27/2007)	NT	28.6 (n=7)
	Sample 4	6/13/2007	F1 (6/1/2007)	F2 (6/10/2007)	NT	25 (n=4)
	Sample 5	6/27/2007	F2 (6/18/2007)	F3 (6/25/2007)	NT	100 (n=1)
	Sample 6	7/11/2007	F3 (7/5/2007)	F4 (7/9/2007)	NT	NT
	Sample 7	-	-	-	-	-
						Total 25.6 (n=39)
15A	Transplant	4/17/2007	-	-	-	-
	Sample 1	5/2/2007	-	-	-	-
	Sample 2	5/15/2007	F0	F0	NT	NT
	Sample 3	5/30/2007	F0	F1 (5/27/2007)	NT	0 (n=1)
	Sample 4	6/13/2007	F1 (6/1/2007)	F2 (6/10/2007)	100 (n=1)	12.5 (n=8)
	Sample 5	6/27/2007	F2 (6/18/2007)	F3 (6/25/2007)	NT	0 (n=19)
	Sample 6	7/11/2007	F3 (7/5/2007)	F4 (7/9/2007)	NT	25 (n=16)
	Sample 7	7/25/2007	F4 (7/19/2007)	F4 (7/21/2007)	NT	0 (n=1)
					Total 100 (n=1)	Total 11.1 (n=45)
15B	Transplant	4/17/2007	-	-	-	-
	Sample 1	5/2/2007	-	-	-	-
	Sample 2	5/15/2007	F0	F0	NT	NT
	Sample 3	5/30/2007	F0	F1 (5/27/2007)	NT	0 (n=1)
	Sample 4	6/13/2007	F1 (6/1/2007)	F2 (6/10/2007)	NT	21.4 (n=14)
	Sample 5	6/27/2007	F2 (6/18/2007)	F3 (6/25/2007)	NT	11.8 (n=17)
	Sample 6	7/11/2007	F3 (7/5/2007)	F4 (7/9/2007)	0 (n=1)	41.0 (n=39)
	Sample 7	7/25/2007	F4 (7/19/2007)	F4 (7/21/2007)	NT	NT
					Total 0 (n=1)	Total 29.6 (n=71)

[1] Generation turnover dates were calculated using the half-sine degree day model with degree day accumulation beginning one week prior to the first observation of TSW within a given plot (TSW symptom expression typically occurs one or more weeks after initial infection). The first sample date on which TSW was observed within a given plot is indicated in bold. [2] PLDA = Petunia leaf disk assay. This assay was performed using thrips collected from plots as immature insects and reared to adults prior to testing for transmission of TSWV. Each thrips was placed on a separate leaf disk. NT indicates that no immature thrips were collected from foliage or blossom samples. Total indicates the overall percentage of all thrips that transmitted out of the total (N) number of thrips collected during the season.

Table 7. Logistic regression model parameters selected using stepwise regression to relate TSW diseased plants from previous periods in 2006 tomato plots to plants that changed from asymptomatic to diseased for a given sample period.

Model	Quantification of Infected Neighbors	Sample Period[1]	Parameters[2]	Model Chi-Square (Maximum Likelihood)	Model P-value	df
Cauchy distribution	Raw number	7	-4.51 + 3.05*S4R4 + 2.10*S5R1	236	< 0.0001	2
Cauchy distribution	Raw number	6	-3.50 + 1.73*S3R9 + 0.93*S4R6 + 1.2*S5R1	108.6	< 0.0001	3
Cauchy distribution	Raw number	5	-1.96 + 1.95*S3R6 + 0.66*S4R7	109	< 0.0001	2

[1]Only late season (sample periods 5-7) models are presented because these are the sample periods during which it is reasonable to expect to observe secondary spread of TSWV based on adult generation turnover date calculations and length of time for plants to express TSW symptoms once infected. [2]S*i*R*j* = Infected neighbor data from sample period *i* within *j* row spaces.

Table 8. Logistic regression model parameters selected using stepwise regression to relate TSW diseased plants from previous periods in 2007 tomato plots to plants that changed from asymptomatic to diseased for a given sample period.

Model	Quantification of Infected Neighbors	Sample Period[1]	Parameters[2]	Model Chi-Square (Maximum Likelihood)	Model P-value	df
Cauchy distribution	Raw number	7	-3.54 + 1.66*S4R8	21.7	< 0.0001	1
Cauchy distribution	Raw number	6	-2.85 + 1.81*S4R6 + 1.00*S5R1	38.9	< 0.0001	2
Cauchy distribution	Raw number	5	-2.53 + 2.26*S4R6	40.4	< 0.0001	1

[1]Only late season (sample periods 5-7) models are presented because these are the sample periods during which it is reasonable to expect to observe secondary spread of TSWV based on adult generation turnover date calculations and length of time for plants to express TSW symptoms once infected. [2]S*i*R*j* = Infected neighbor data from sample period *i* within *j* row spaces.

Table 9. Logistic regression model parameters selected using stepwise regression to relate TSW diseased plants from previous periods in 2006 pepper plots to plants that changed from asymptomatic to diseased for a given sample period.

Model	Quantification of Infected Neighbors	Sample Period[1]	Parameters[2]	Model Chi-Square (Maximum Likelihood)	Model P-value	df
Count	Raw number	6	-4.20 - 0.01*S3R8 + 0.002*S4R9 + 0.02*S5R5	139.8	< 0.0001	3
Count	Raw number	5	-0.48 - 0.01*CropDD2 + 0.06*S2R6 - 0.05*S3R5 + 0.04*S4R5	508.4	< 0.0001	4

[1]Only late season (sample periods 5-6) models are presented because these are the sample periods during which it is reasonable to expect to observe secondary spread of TSWV based on adult generation turnover date calculations and length of time for plants to express TSW symptoms once infected. [2]S*i*R*j* = Infected neighbor data from sample period *i* within *j* row spaces.

Table 10. Logistic regression model parameters selected using stepwise regression to relate TSW diseased plants from previous periods in 2007 pepper plots to plants that changed from asymptomatic to diseased for a given sample period.

Model	Quantification of Infected Neighbors	Sample Period[1]	Parameters[2]	Model Chi-Square (Maximum Likelihood)	Model P-value	df
Count	Proportion of all neighbors	7	1.36 + 3.15*S2R7 + 1.77*S3R5 - 0.29*S5R5	32	< 0.0001	3
Count	Proportion of all neighbors	6	-26.03 + 0.03*CropDD5 - 2.13*S1R8 - 0.63*S2R5 - 0.41*S3R9 + 0.21*S4R9 + 0.35*S5R5	1820.6	< 0.0001	6
Count	Proportion of all neighbors	5	10.25 - 0.04*CropDD3 - 6.28*S1R9 + 1.20*S2R6 - 0.63*S3R9 + 0.31*S4R9	1279.4	< 0.0001	5

[1]Only late season (sample periods 5-7) models are presented because these are the sample periods during which it is reasonable to expect to observe secondary spread of TSWV based on adult generation turnover date calculations and length of time for plants to express TSW symptoms once infected. [2]S*i*R*j* = Infected neighbor data from sample period *i* within *j* row spaces.

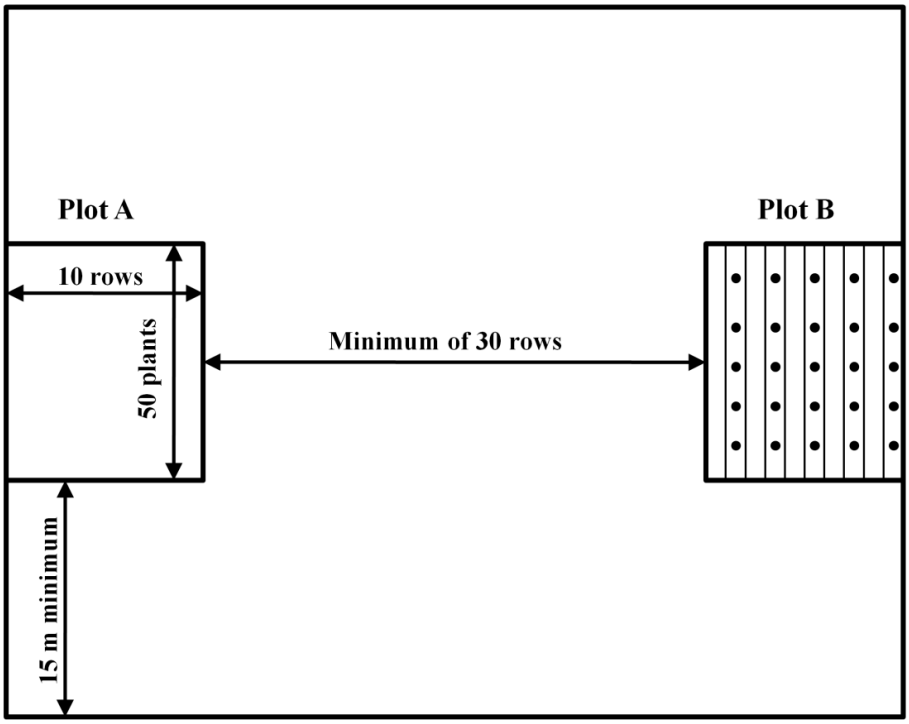


Figure 1. Generalized plot layout for an individual field. Sticky traps that were interior to a plot are represented by dots.

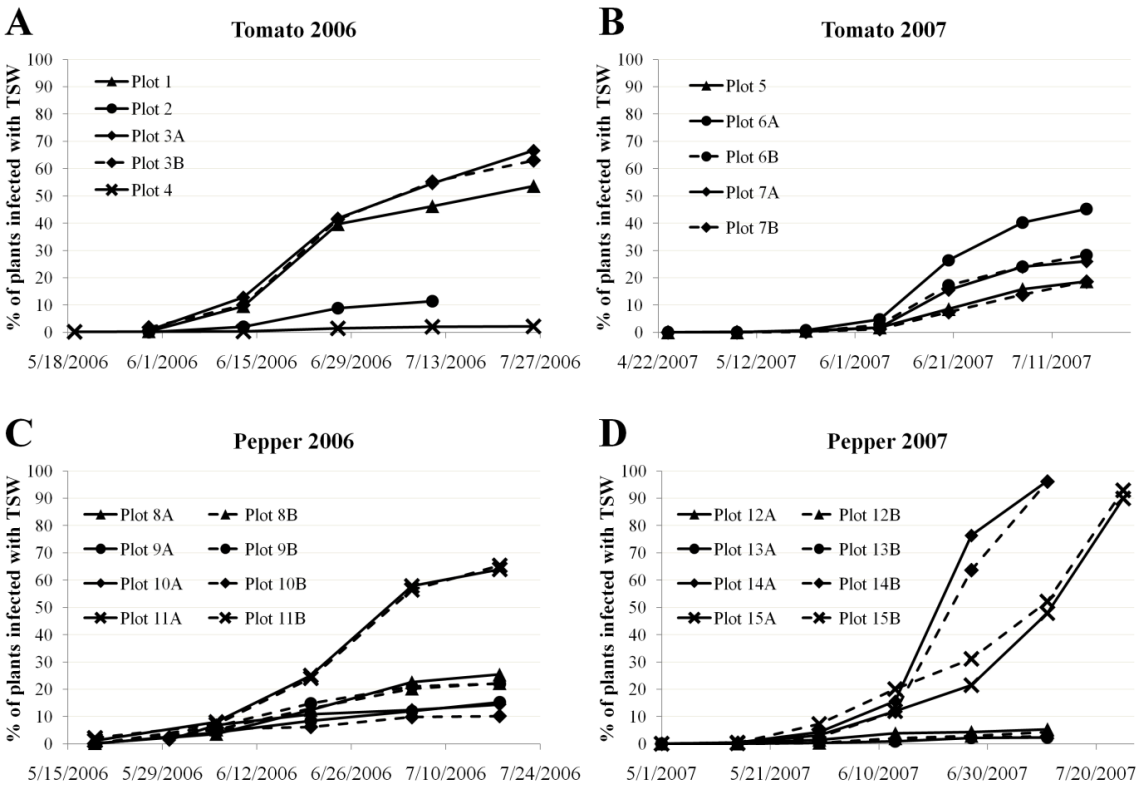


Figure 2. Disease progress curves for tomato and pepper plots.

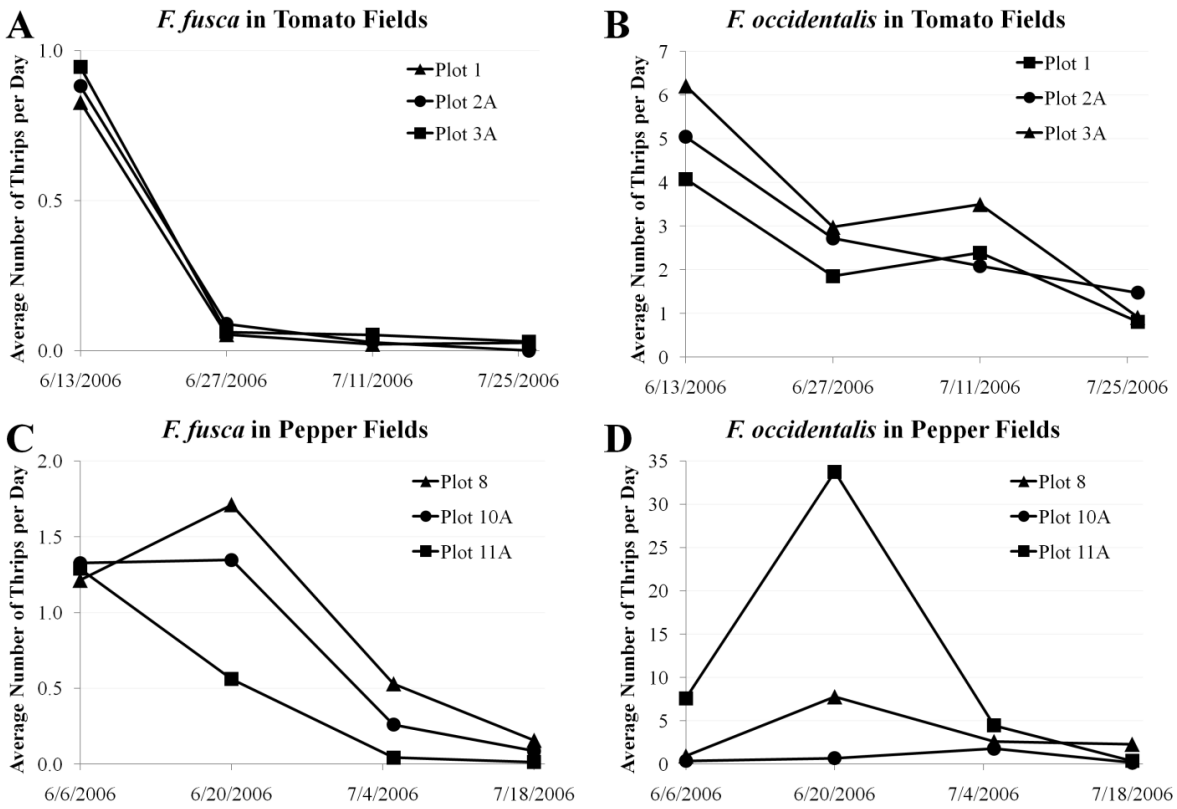


Figure 3. Vector thrips captured on internal sticky trap cards in 2006 tomato and pepper plots. Thrips capture data are standardized to the sticky trap surface area of round sticky traps.

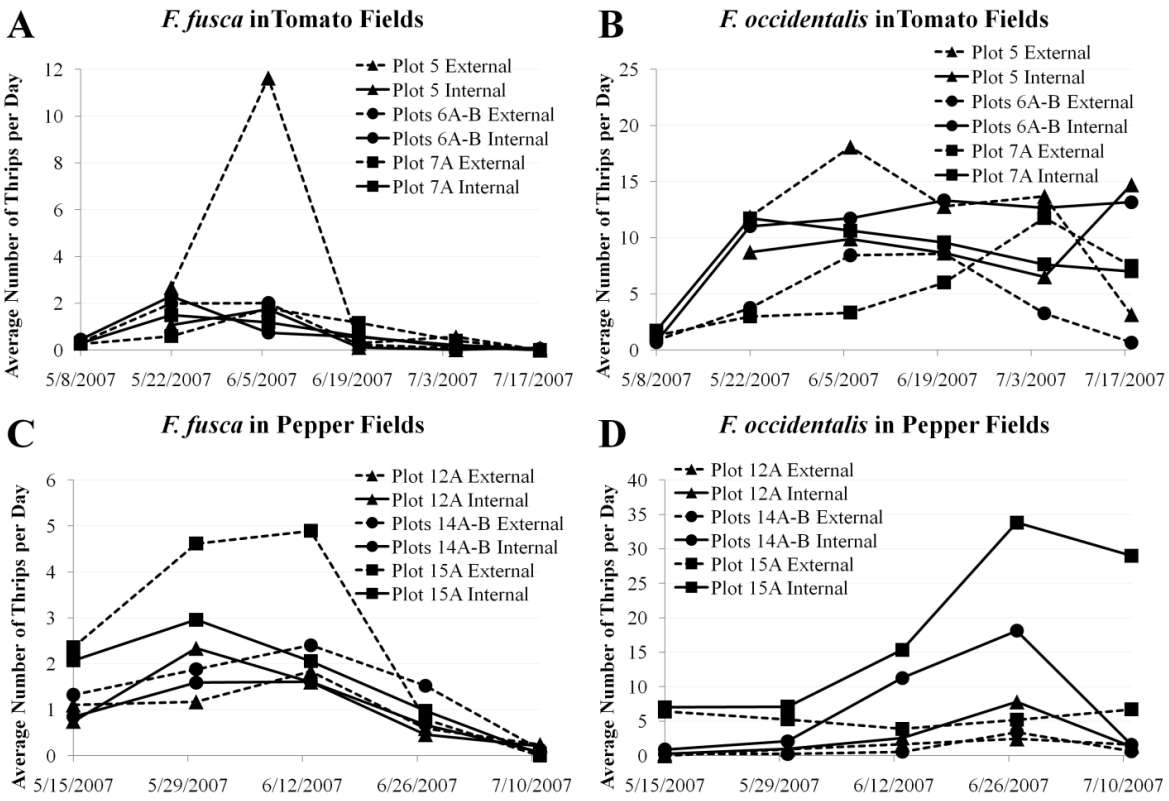


Figure 4. Vector thrips captured on internal sticky trap cards and external round sticky traps in 2007 tomato and pepper plots. Thrips capture data from internal sticky cards are standardized to the sticky trap surface area of round sticky traps.

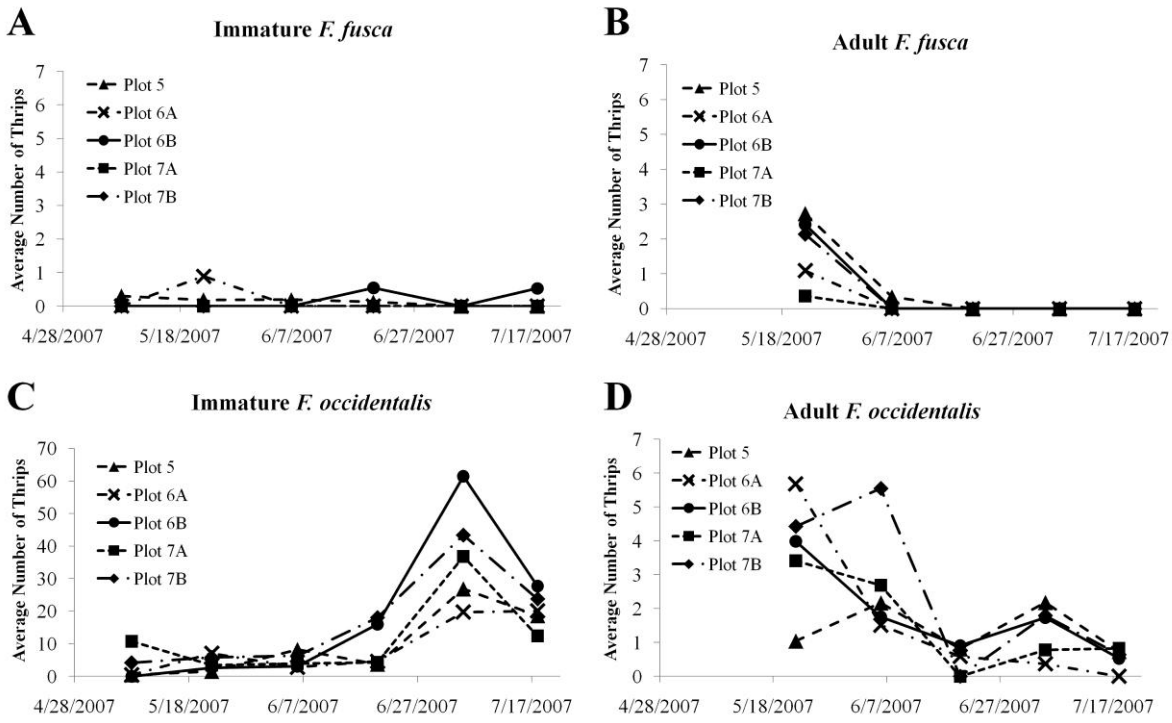


Figure 5. Average number of thrips vectors recovered from tomato foliage samples standardized to 5 g dry weight of foliage. Ten foliage samples per plot were collected on each date.

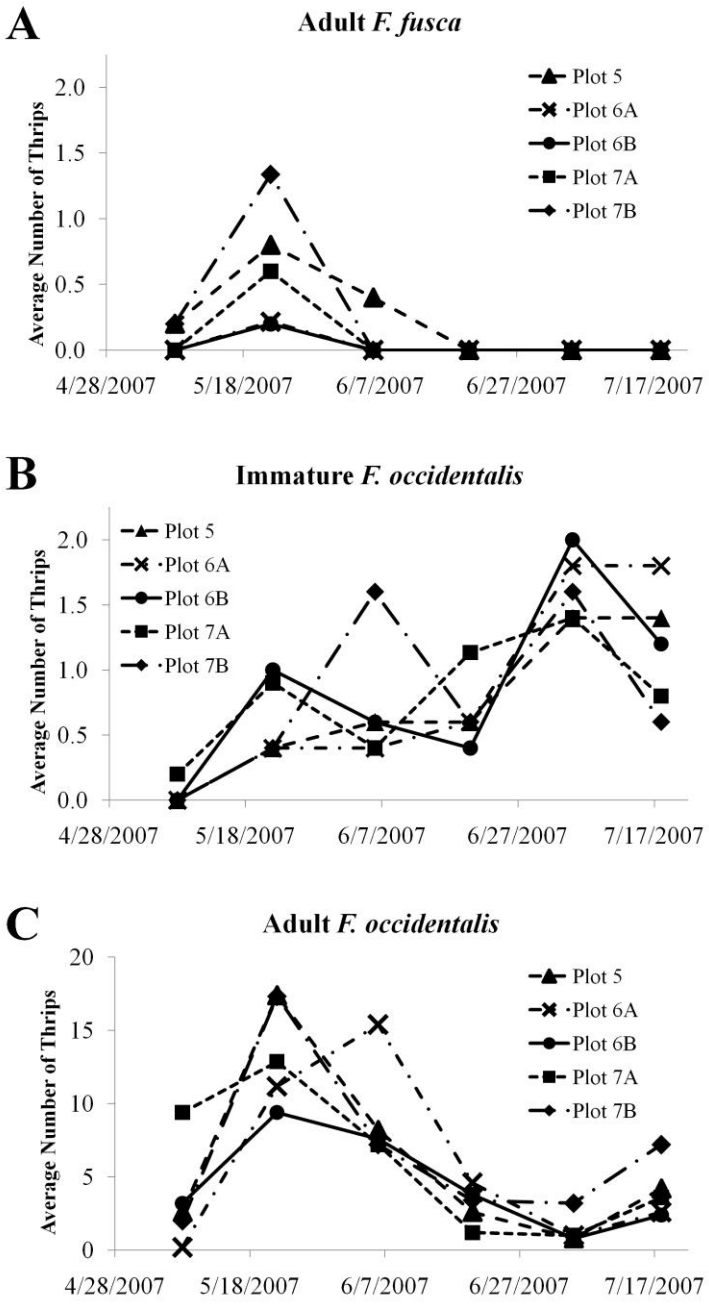


Figure 6. Average number of thrips vectors recovered from ten tomato blossoms per sample. Five samples of ten blossoms were collected from each plot on each date. No immature *F. fusca* were collected from any of the samples.

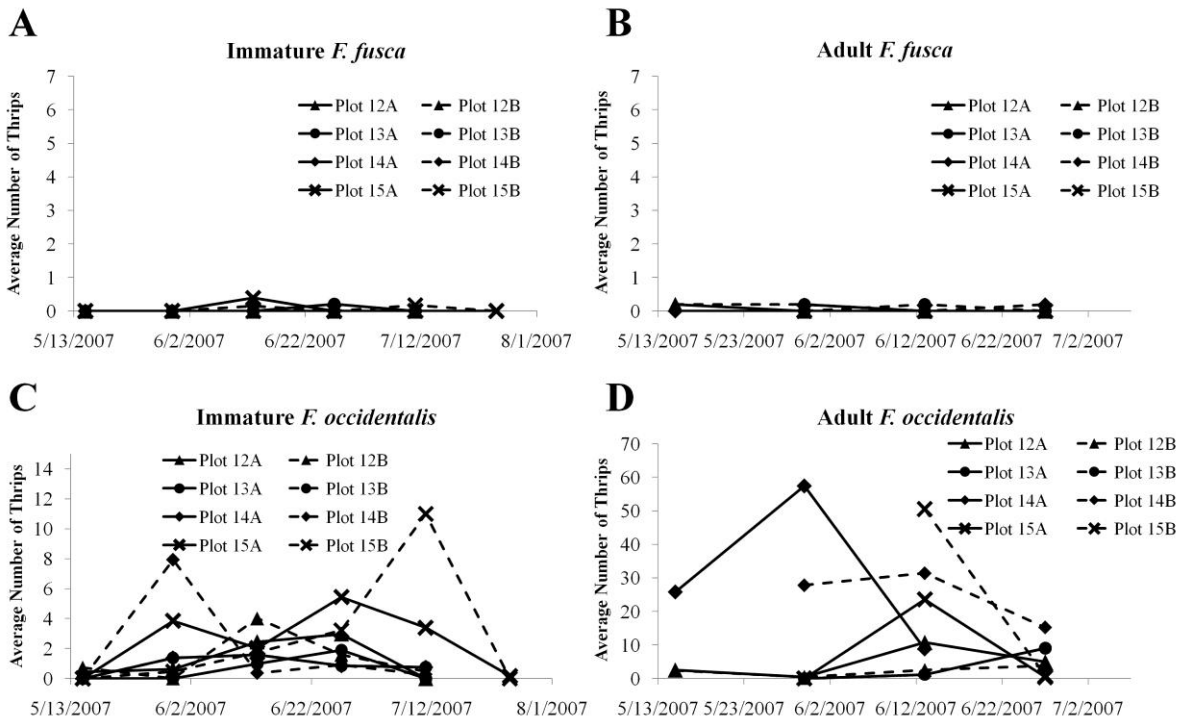


Figure 7. Average number of thrips vectors recovered from pepper foliage samples standardized to 5 g dry weight of foliage. Ten foliage samples per plot were collected on each date.

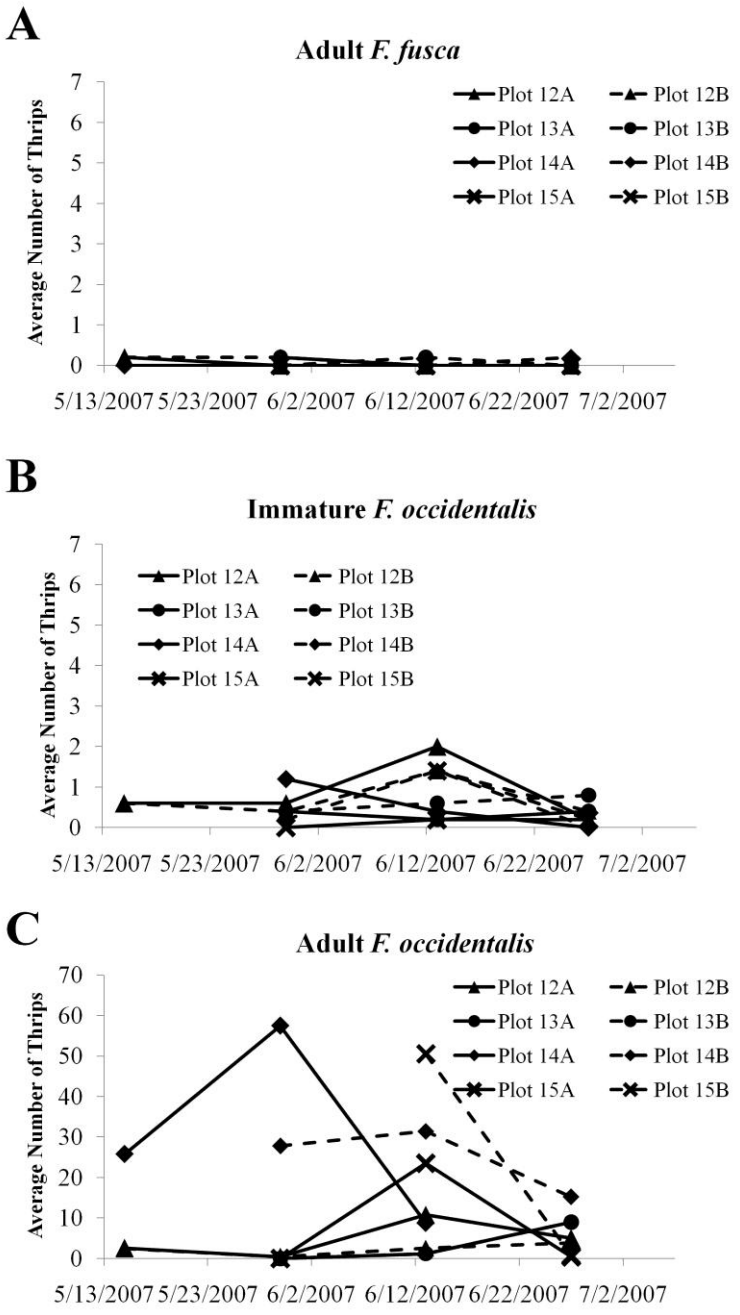


Figure 8. Average number of thrips vectors recovered from ten pepper blossoms per sample. Five samples of five blossoms per location were collected from each plot on each date. No immature *F. fusca* were collected from any of the samples.

Discussion

Regional temperature and precipitation explain the majority of variation in average *F. fusca* captured on sticky traps, but regional models do not accurately describe the number of *F. fusca* captured on sticky traps from individual farms (Morsello 2007). The importance of field and field margin characteristics were studied to better understand thrips and TSWV dynamics on a farm scale. *F. fusca* and *F. occidentalis* populations increase on winter annual weeds and thrips disperse to summer annual weeds and crops as the winter weeds begin to senesce (Eckel et al. 1996, Groves et al. 2001, 2003, Morsello et al. 2009). Because experiments showed that the younger pepper transplants are when exposed to viruliferous thrips the more susceptible they are to TSWV infection, timing of TSWV vector dispersal with regard to transplant of TSWV susceptible crops, can have a profound impact on TSW prevalence within a given field. Therefore, it was important to understand if thrips vectors originate from local weed sources and disperse short distances within a field. If so, management of weedy margins could play a key role in controlling the spread of TSWV. Originally, it was hypothesized that a gradient of decreasing *F. fusca* captures on sticky traps would be observed with increasing distance from weedy field margins, which were the nearest *F. fusca* hosts. However, observed patterns were contrary to the hypothesis. Although an increase in the number of *F. fusca* captured or TSW prevalence with proximity to weedy field margins was not observed, weedy margins adjacent to a field can still be important to thrips and TSWV pressure in a field because some farm practices can induce thrips dispersal from weed hosts, and if dispersal is triggered, when TSWV-susceptible crops are young, TSWV spread may be exacerbated compared to a scenario in which thrips dispersed naturally from senescing weeds. For pepper, transmission of TSWV by *F. fusca* decreased by 50%

after three to nine days post transplant, and both tobacco (Mandal et al. 2007) and peanut (Mandal et al. 2001) exhibit mature-plant resistance to TSWV. It is uncertain whether or not tomato becomes more resistant to TSWV with age. Multiple attempts to study whether or not tomato plants exhibit mature-plant resistance to TSWV failed. A field trial using multiple ages of tomato plant and ambient thrips and TSWV pressure failed due to a lack of virus pressure during the growing season. TSWV transmission to tomato plants in a field trial with a controlled release of viruliferous thrips to multiple ages of plants was ruined by a tropical storm, and a greenhouse experiment failed when the TSWV isolate used mutated and was no longer thrips transmissible. However, because pepper, tobacco, and peanut all show mature-plant resistance to TSWV, it is advisable that growers consider that tomato plants are likely to exhibit mature-plant resistance (and therefore much greater susceptibility at transplant age) and avoid increasing thrips and TSWV exposure when tomato plants are young. Since killing winter weeds using glyphosate can increase *F. fusca* dispersal from weeds, it is advisable avoid managing winter weeds in the late spring using glyphosate if any crops susceptible to TSWV will be transplanted within four weeks of weed management in nearby fields. If herbicide must be used to manage winter weeds less than four weeks prior to transplant of a susceptible crop, paraquat may be a better alternative to glyphosate because increased dispersal lasted only one week following paraquat treatment. Alternatively, winter weeds may be disked at any time in spring without increasing dispersal of *F. fusca*.

Data collected to check for secondary spread of TSW within tomato and pepper fields showed that sufficient developmental time passes between the initial TSW observation and final harvest for both *F. fusca* and *F. occidentalis* progeny to hatch on infected plants,

acquire TSWV, become adults, transmit TSWV, and for the newly infected plants to show TSW symptoms. Sticky trap, foliage, and blossom data indicate that *F. fusca* are transient and do not establish resident populations within tomato and pepper fields, but *F. occidentalis* does colonize at least some fields of both crops. Therefore, *F. fusca* is unlikely to contribute to secondary spread within tomato and pepper fields. Based on thrips census data and an assumed foliage dry weight of 100 g per plant, the estimated number of potentially viruliferous *F. occidentalis* produced per generation of progeny that could contribute to secondary spread per diseased tomato or pepper plant ranged from 4-41 and 12-41 individuals, respectively. Regression models relating change in plant disease status to diseased neighbors did not provide evidence of secondary spread in pepper fields and provided only very weak evidence for one year of tomato observations. However, the potential for secondary spread of TSW by *F. occidentalis* cannot be ruled out even if models did not provide strong or any evidence of secondary spread because underlying assumptions of secondary spread patterns may be incorrect for the system studied. Six reasons that patterns of secondary spread might not be observed were discussed in Chapter 4 and are summarized here: 1. TSW patterns may not reflect thrips dispersal patterns. 2. TSW symptoms that appear during the same sample period do not necessarily reflect infection that occurred at the same time. 3. Multiple vector species may have different dispersal patterns and therefore create two separate patterns of TSW disease spread that, when overlaid on one another, obscure one or both patterns. 4. If primary spread occurs continuously throughout the season, the patterns of primary and secondary TSW spread may obscure each other. 5. It is possible that patterns of secondary spread are not detectable due to the plot sizes used in

these studies. 6. Expected patterns of secondary spread such as diseased neighbor effects assume that thrips vectors that contribute to secondary TSWV spread move and transmit TSW from origin points to susceptible plants that are relatively close, but this might not be true. The presence of resident, competent *F. occidentalis* vectors for 4-8 weeks after initial TSW was observed substantiates the possibility of secondary spread of TSW in tomato and pepper fields.

Increased dispersal of *F. fusca* from weedy patches managed with glyphosate likely does not increase the potential for secondary spread of TSWV within tomato and pepper plots because there is no evidence that *F. fusca* colonize the crops and establish resident populations. *F. occidentalis* were not included in the weed management study because *F. fusca* had been considered the primary vector of TSWV in North Carolina. However, if *F. occidentalis* were present within managed weeds, it is likely that *F. occidentalis* would disperse as host quality declined as a result of herbicide application. Because *F. occidentalis* may establish resident populations within tomato and pepper fields and have the potential to contribute to late-season secondary spread of TSWV, management of winter weeds that may increase *F. occidentalis* dispersal has the potential to promote early-season colonization of crops and exacerbate secondary spread of TSWV. The earlier a tomato or pepper field is colonized by *F. occidentalis*, the more developmental time passes, allowing for additional population increase and turnover of generations.

Although *F. occidentalis* is a known vector of TSWV in North Carolina, it was surprising to learn that sticky traps external to the field, but only a few meters from tomato and pepper field edges, captured relatively few *F. occidentalis* compared to traps internal to

the fields. The importance of *F. occidentalis* as a TSWV vector in North Carolina may have been underestimated in the past because the majority of thrips sticky traps collected by North Carolina State University researchers since 1997 have been along field margins. In the future, it is important that experiments include thrips samples internal to a field, especially for tomato and pepper studies. Presence of tomato and pepper blossoms (and therefore pollen) throughout the growing season may be a reason that *F. occidentalis* colonize tomato and pepper fields since *F. occidentalis* prefer to dwell in blossoms rather than on foliage and they readily consume pollen (Riley et al. 2007). Findings that *F. occidentalis* become resident in tomato and pepper fields and that the potential for secondary spread exists warrant additional experiments to study whether pesticide use or biocontrol measures affect final prevalence of TSW and yields within fields containing resident *F. occidentalis* populations, and under what conditions it is economically viable to control resident *F. occidentalis* populations. Although not explicitly designed to assess the impact of controlling *F. occidentalis* populations, Riley and Pappu found that insecticide treatments reduced *F. occidentalis* on sticky traps and in blossom samples and increased marketable tomato yield (2000). However, immature thrips were not reared and identified to species, and presence of other vector species complicates interpretation of results with regard to secondary spread of TSWV. Experiments employing controlled release of *F. occidentalis* on infected crop plants surrounded by healthy plants with purposeful exclusion of *F. fusca* from experimental plots could help clarify whether or not *F. occidentalis* cause secondary spread of TSWV within tomato and pepper fields.

References Cited

Eckel, C. S., K. Cho, J. F. Walgenbach, G. G. Kennedy, and J. W. Moyer. 1996. Variation in thrips species composition in field crops and implications for tomato spotted wilt epidemiology in North Carolina. Entomol. Exp. Appl. 78: 19-29.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2001. Overwintering of *Frankliniella fusca* (Thysanoptera: Thripidae) on winter annual weeds infested with tomato spotted wilt virus and patterns of virus movement between susceptible hosts. Phytopathol. 91: 891-899.

Groves, R. L., J. F. Walgenbach, J. W. Moyer, and G. G. Kennedy. 2003. Seasonal dispersal patterns of *Frankliniella fusca* (Thysanoptera: Thripidae) and tomato spotted wilt virus occurrence in central and eastern North Carolina. J. Econ. Entomol. 96: 1-11.

Mandal, B., H. R. Pappu, and A. K. Culbreath. 2001. Factors affecting mechanical transmission of tomato spotted wilt virus to peanut (*Arachis hypogaea*). Plant Dis. 85: 1259-1263.

Mandal, B., M. L. Wells, N. Martinez-Ochoa, A. S. Csinos, and H. R. Pappu. 2007. Symptom development and distribution of tomato spotted wilt virus in flue-cured tobacco. Ann. Appl. Biol. 151: 67-75.

Morsello, S. C. 2007. The role of temperature and precipitation on Thrips populations in relation to the epidemiology of tomato spotted wilt virus. Ph.D. dissertation. North Carolina State University, Raleigh, NC.

Morsello, S. C. and G. G. Kennedy. 2009. Spring temperature and precipitation affect tobacco thrips, *Frankliniella fusca*, population growth and tomato spotted wilt virus spread within patches of the winter annual weed *Stellaria media.* Entomol. Exp. Appl. 130: 138-148.

Riley, D. G., A. Chitturi, and A. N. Sparks, Jr. 2007. Does natural deposition of pine pollen affect the ovipositional behavior of *Frankliniella occidentalis* and *Frankliniella fusca*? Entomologia Experimentalis et Applicata. 124: 133-141.

Riley, D. G. and H. R. Pappu. 2000. Evaluation of tactics for management of thrips-vectored tomato spotted wilt virus in tomato. Plant Dis. 84: 847-852.

Riley, D. G. and H. R. Pappu. 2004. Tactics for management of thrips (Thysanoptera: Thripidae) and tomato spotted wilt virus in tomato. J. Econ. Entomol. 97: 1648-1658.