

# The influence of temperature and precipitation on spring dispersal of *Frankliniella fusca* changes as the season progresses

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## Abstract

Effects of temperature and precipitation on spring dispersal patterns of *Frankliniella fusca* (Hinds) (Thysanoptera: Thripidae) caught on yellow sticky traps were estimated in central and eastern North Carolina and eastern Virginia, USA, from 1997 to 2001, and in 2004 and 2007. Data were collected from 44 sites within 14 locations over 7 years, resulting in 30 location-year data combinations. The following independent variables were examined to determine their relationship to the number of *F. fusca* caught on sticky traps during specified time intervals: cumulative degree days (base 10.5 °C) from 1 November to the start of each trapping interval (DD), number of days with temperatures favorable for flight during each trapping interval (DTFF), and an index of rainfall during specific intervals prior to and during the trapping interval (RI). Regression models that contained various combinations of these variables explained 62, 79, 74, and 68% of the variation in the number of dispersing *F. fusca* captured during 1–15 April, 16–30 April, 1–15 May, and 16–31 May, respectively. The results provide strong evidence that the suppressive effects of precipitation on growth of local populations developing during late winter and early spring are subsequently manifest at the landscape scale as reductions in the populations of dispersing adults that may persist for as long as 5–6 weeks after the precipitation occurs.

## Introduction

Massive dispersal of thrips populations from winter and early spring hosts frequently results in damaging infestations on numerous crops. Identifying and characterizing the influence of factors that affect the timing of dispersal and the size of the dispersing populations are important to understanding the population dynamics of these thrips and may lead to the identification of conditions that are highly conducive to the occurrence of damaging thrips infestations.

*Frankliniella fusca* (Hinds) (Thysanoptera: Thripidae), the tobacco thrips, is an important, early-season pest

affecting numerous crops in the southeastern USA, including pepper, tomato, tobacco, and peanut. It frequently causes significant losses in these crops because of feeding damage or by transmission of Tomato spotted wilt virus (*Bunyaviridae*, genus *Tospovirus*, TSWV) (Barbour & Brandenburg, 1994; Cho et al., 1995; Brecke et al., 1996; Eckel et al., 1996; Gitaitis et al., 1998; McPherson et al., 1999; Groves et al., 2003; Nault et al., 2003). Losses are greatest when feeding damage or TSWV infection occurs during the first several weeks following transplanting (pepper, tomato, and tobacco) or seedling emergence (peanut) (Parrella & Lewis, 1997; Moriones et al., 1998; Mandal et al., 2001; Beaudoin & Kennedy, 2009). Thus, planting date in relation to the magnitude and occurrence of dispersing *F. fusca* populations can greatly affect the amount of losses to thrips damage and tomato spotted wilt prevalence.

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In North Carolina, USA, *F. fusca* disperse in the fall from summer to winter hosts, which consist largely of winter annuals growing in and around agricultural fields (Cho et al., 1995; Groves et al., 2001, 2002). The thrips remain active throughout the winter with egg and larval development occurring whenever temperatures exceed the developmental threshold of 10.5 °C (Lowry et al., 1992; Groves et al., 2001). As temperatures warm and winter annual weeds begin to grow rapidly in late winter and early spring, *F. fusca* populations may increase rapidly and begin to disperse (Groves et al., 2001, 2003; Morsello & Kennedy, 2009). There is considerable spatial and temporal variation in *F. fusca* dispersal from winter hosts to crops and summer hosts each year. Significant dispersal by *F. fusca* from winter hosts begins in late March or early April and dispersing populations may peak in late May but more typically peak in June (Groves et al., 2001, 2003; Morsello et al., 2008).

Temperature and precipitation exert a strong influence on thrips populations (Kirk, 1997). Temperature affects the development rate of insects and hence their population dynamics (Logan et al., 1976). It also influences the growth and development rate of their host plants, which may affect host availability and suitability for thrips (e.g., Davidson & Andrewartha, 1948). Temperature affects thrips dispersal because temperatures above 17–21 °C are generally required for flight (Lewis, 1997). Because the lower temperature threshold for flight is above that required for development, large populations of adult thrips can develop on plants during spring when temperatures fluctuate between the development and flight thresholds (Lewis, 1964).

Rainfall affects thrips populations both negatively and positively. It can suppress populations by killing larvae, and thrips populations so affected often recover slowly (Bailey, 1933, 1934; Kirk, 1997; Morsello & Kennedy, 2009). Rainfall suppresses thrips dispersal by suppressing flight (Lewis, 1997). However, by maintaining adequate soil moisture, rainfall can positively influence thrips populations by fostering plant growth and enhancing pupal survival (Davidson & Andrewartha, 1948). Using a regression approach, Morsello et al. (2008) found that cumulative developmental degree days, amount of precipitation, and the number of days with measurable precipitation from 1 January explained 70 and 55% of the total variation in total number of dispersing *F. fusca* captured on yellow sticky traps in North Carolina through 10 May and 31 May, respectively. In a subsequent study, Morsello & Kennedy (2009) documented the suppressive effects of natural and simulated rainfall on growth of *F. fusca* populations developing on their overwintering host plants in late winter and spring. Using small plot field experiments, they demon-

strated that the degree to which population growth was suppressed by precipitation depended on the timing, amount, and duration of precipitation events.

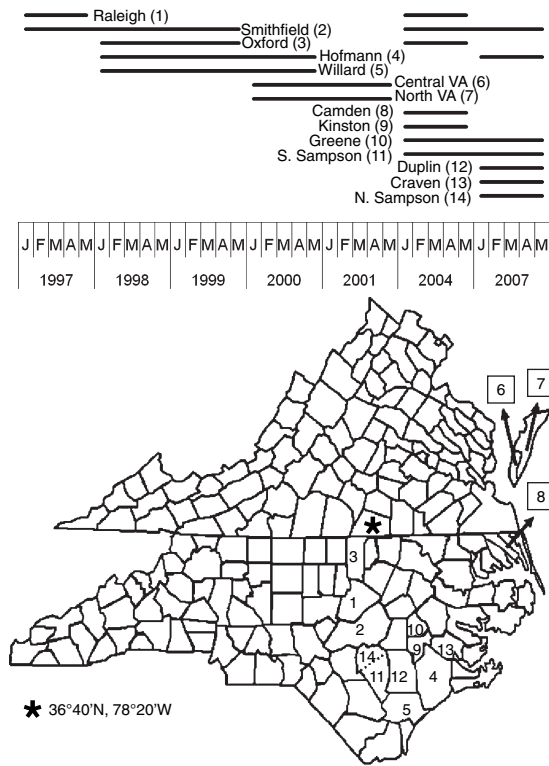
In this study, we address the question of whether and to what extent the effects of temperature and rainfall on population growth of *F. fusca* at the local level reported by Morsello & Kennedy (2009) can be observed as changes in populations of dispersing adults at the landscape level. Based on the previously described effects of temperature and rainfall on the growth and dispersal of thrips populations in general and on *F. fusca* in particular, we hypothesized that, on a landscape scale, spatial and within-season temporal variation in the number of dispersing *F. fusca* caught on sticky traps in spring are related to winter and spring temperatures and the timing and amount of rainfall that suppresses thrips populations on their host plants during specific periods prior to the trapping interval. We further hypothesized that temperatures and rainfall during the trapping period that suppress flight would also be related to the number of *F. fusca* caught on traps. Here, we report results from a series of regression analyses that test these hypotheses by examining the relationship between temperature and specific periods of precipitation during winter and spring on the number of *F. fusca* adults captured on yellow sticky traps placed around and in commercial crop fields during periods of spring dispersal.

## Materials and methods

### Aerial trap collection

Spring dispersal of *F. fusca* was monitored from 1997 to 2001, and in 2004 and 2007 at 44 field sites in central and eastern North Carolina and eastern Virginia, using yellow sticky traps positioned along the field margins or within crop fields. Not all field sites were monitored in each year (Figure 1). Each year, trapping was initiated at all sites before crops were planted.

In North Carolina, selected field sites were planted to tobacco, cotton, or soybean and in Virginia, the fields were planted to tomato during the trapping period. Traps in North Carolina consisted of cylindrical PVC pipe (7.5 cm length × 2.5 cm diameter) painted yellow (John Deere Yellow Model 981<sup>®</sup>; Spray Products, Norristown, PA, USA) and wrapped with Tanglefoot-coated transparent plastic wrap (Great Lakes Integrated Pest Management, Vestaburg, MI, USA) that resulted in 55.7 cm<sup>2</sup> of sticky area. Traps were fastened to a wooden dowel and set at a height of 1 m above the soil. From 1997 to 2001 at each field site, four traps, separated by 10 m, were arranged in a linear pattern along one side of the field to avoid interference with any cultural practices. At each field site during 2004 and 2007, 4–6 traps were separated by >10 m and



**Figure 1** *Frankliniella fusca* adult trapping intervals for each of the 14 locations over 7 years associated with different NOAA weather stations in central and eastern North Carolina and eastern Virginia, resulted in 30 location years (not all locations had traps each year). Values in parentheses correspond to map positions.

arranged around field perimeters, with at least one trap on each field edge, to avoid interference with any cultural practices. Vegetation within ca. 0.4 m<sup>2</sup> surrounding each trap was maintained at a height of <5 cm above the soil surface over the trapping interval using a motorized string trimmer. Between 1 April and 31 May of each year, traps were collected and replaced at approximately 7-day intervals. Recovered traps were returned to the laboratory where the Tanglefoot-coated plastic wraps were removed from the PVC cylinders and sandwiched between two pieces of transparent plastic wrap (S.C. Johnson & Son, Racine, WI, USA).

In Virginia, yellow sticky cards with 193.5 cm<sup>2</sup> of sticky area (7.6 × 12.7 cm, both sides exposed) were fastened to trellis supports in tomato fields and adjusted weekly to just above the height of the growing plant canopy. At each field location, cards were placed in three rows: the middle row had one card and was flanked by rows that each had two cards (five cards total). Rows containing cards were separated by >10 m. All cards were within 20 m of field edges. Traps were replaced at 7-day intervals and returned to the

laboratory for processing (Nault et al., 2003). Data from VA traps were multiplied by 0.29 per trap to adjust for the larger surface area of the traps used in Virginia.

**Thrips identification**

When 25 or fewer adult thrips were collected on a trap, all thrips were identified to species. When there were more than 25 thrips on a trap, the total number of adult thrips was counted and a random subsample of 25 thrips was removed for identification to species. Individual thrips recovered for identification were mounted on a microscope slide. Species of adult thrips were determined using a key to adult thrips of the Terebrantia suborder (Palmer et al., 1992). The proportion of each species within the subsample was then multiplied by the total number of thrips captured on that trap to estimate the total number of each species present on the trap. Voucher specimens are held at the North Carolina State University Museum and Eastern Shore Agricultural Research and Extension Center near Painter, Virginia.

**Thrips trapping intervals of interest**

The period from 1 April through 31 May, during which crops such as tomato, tobacco, pepper, peanut, and cotton are most affected by *F. fusca* infestations in North Carolina, was divided into four consecutive trapping intervals of interest: 1–15 April, 16–30 April, 1–15 May, and 16–31 May. Tomato, tobacco, and pepper may be transplanted throughout this period whereas peanut and cotton are planted as seeds in early May with seedling emergence in mid-May. As these crops grow, they become increasingly tolerant of thrips damage and in the case of tomato, tobacco, pepper, and peanut, to the effects of TSWV (Moriones et al., 1998; Mandal et al., 2007; Beaudoin & Kennedy, 2009). Thus, when considered in relation to location and planting date for a given crop, these intervals reflect different potentials for crop exposure to *F. fusca* dispersing from winter hosts in spring. They also span the period when populations of dispersing *F. fusca* are changing rapidly.

**Weather data**

All field sites were grouped into locations based on proximity to each other and assigned weather data from the nearest National Oceanic and Atmospheric Administration (NOAA) (<http://cdo.ncdc.noaa.gov/dly/DLY>) weather station. No field site was greater than 25 miles from another field site grouped within the same location and only one weather station was used per location (Morsello et al., 2008). Daily degree days (DD) were calculated based on a lower developmental threshold value of 10.5 °C for *F. fusca* (Lowry et al., 1992) using the half-day sine

wave method (Higley et al., 1986). Degree days were summed from 1 November through 31 March, 15 April, 30 April, and 15 May for each year at each weather station. November first was chosen as the start date for degree day accumulation based on fall trapping data from 1997 through 2000 (Groves et al., 2003), in which 1 November was the estimated mean midpoint of *F. fusca* dispersal from summer hosts to winter hosts. We were not able to use location-specific fall dispersal midpoints as a biofix because fall trapping data were not available for all locations in some years or for any locations in 2004 and 2007. The dates 31 March, 15 April, 30 April, and 15 May were chosen as end dates to account for all degree day accumulation prior to the beginning of each specific *F. fusca* trapping interval. Days with temperatures favorable for flight (DTFF) during each dispersal interval of interest were estimated by summing the number of days that the reported maximum temperature exceeded 20 °C during each of the trapping intervals (1–15 April, 16–30 April, 1–15 May, and 16–31 May). The temperature of 20 °C was chosen as a conservative flight threshold to test the importance of environmental favorability for flight based on the estimated 17–21 °C flight threshold range reported for most thrips species (Lewis, 1997).

Because previous research had indicated that precipitation during specific intervals had a greater effect on *F. fusca* populations on overwintered hosts than precipitation during other intervals (Morsello & Kennedy, 2009), we examined the effects of rainfall during successive ca. 15-day intervals beginning 1 January. The number of days in which precipitation occurred and the total amount of precipitation occurring during each of the following intervals were calculated from daily precipitation records: 1–15 January, 16–31 January, 1–15 February, 16–28 February, 1–15 March, 16–31 March, 1–15 April, 16–30 April, 1–15 May, and 16–31 May. Because precipitation amount and the number of days with precipitation within these rainfall intervals were highly correlated, these parameters were combined into a single variable termed 'rainfall index' to avoid over-parameterizing the regression model. This was performed by multiplying centimeters of precipitation by the number of days with precipitation that occurred for each interval and location. Combining these variables in this way is consistent with previous findings that prolonged intervals of light precipitation can have as great an effect on thrips as brief periods of heavy precipitation (Morsello & Kennedy, 2009).

#### Statistical analysis

For each sampling date, the estimated number of *F. fusca* was averaged across all traps located within a field site. The estimated number of *F. fusca* collected at each site during

each interval was divided by the number of days between sample dates to estimate the number of *F. fusca* per trap per day because the approximately 7-day trapping intervals were not the same over each of the 7 years. For each field site in each year, the estimated number of *F. fusca* per trap per day was summed within the trapping intervals 1–15 April, 16–30 April, 1–15 May, and 16–31 May. For each interval, these values were averaged across field sites within each of the weather station-associated locations (Figure 1) to estimate the mean number of *F. fusca* adults per location trapped during a specified interval. Overall, *F. fusca* were captured at 14 locations over 7 years. Because not all locations were sampled throughout the study, our data set included a total of 30 location-year data combinations (Figure 1).

Data on the mean number of *F. fusca* adults per location trapped during each interval were log transformed, based on an inspection of residuals (SAS 9.1, Proc PLOT) (SAS, 2005), to stabilize variance prior to stepwise regression. The 30 location-years of trapping data were subjected to stepwise regression (SAS 9.1, Proc REG) (SAS, 2005) to test for relationships between the mean number of *F. fusca* adults per location-year captured during each trapping interval (1–15 April, 16–30 April, 1–15 May, and 16–31 May) and the following independent variables: cumulative degree days from 1 November through 1 day prior to the start of the trapping interval (DD); number of days with temperatures favorable for thrips flight during the trapping interval (DTFF); and rainfall index estimates (RI) for successive 13- to 16-day intervals during the period extending from 1 January through the final date of the trapping interval. Each rainfall interval was treated as a separate independent variable. Prior to stepwise regression, correlation of weather variables with mean number of *F. fusca* adults per location was assessed (Proc CORR) (SAS, 2005) for each trapping interval. Only variables for which these correlations were significant ( $P \leq 0.15$ ) were included in the stepwise regression analysis (Table 1). Selecting independent variables to be subjected to stepwise regression analysis using a correlation test prevents reduction of statistical power in the regression analysis. The correlation analysis significance cutoff of  $P \leq 0.15$  is the standard minimum significance cutoff in stepwise regression and allows examination of variables that may have explanatory power once variation due to other variables previously included in the regression model has been accounted for.

The robustness of each of the four trapping interval regression models was assessed using jackknife and bootstrap re-sampling code from the SAS Knowledge Base (SAS, 2007). For the jackknife re-sampling analysis, a leave-one-out approach was used following the examples

**Table 1** Parameters subjected to correlation analysis and those selected for inclusion in stepwise regression analysis for each trapping interval

Trapping interval	Correlation analysis parameters	Stepwise regression parameters
1–15 April	DD <sub>1 Nov–31 Mar</sub> DTFF <sub>1–15 Apr</sub> RI <sub>1–15 Jan</sub> , RI <sub>16–31 Jan</sub> RI <sub>1–15 Feb</sub> , RI <sub>16–28 Feb</sub> RI <sub>1–15 Mar</sub> , RI <sub>16–31 Mar</sub> RI <sub>1–15 Apr</sub>	<b>DD<sub>1 Nov–31 Mar</sub></b> <b>RI<sub>16–31 Mar</sub></b> DTFF <sub>1–15 Apr</sub>
16–30 April	DD <sub>1 Nov–15 Apr</sub> DTFF <sub>16–30 Apr</sub> RI <sub>1–15 Jan</sub> , RI <sub>16–31 Jan</sub> RI <sub>1–15 Feb</sub> , RI <sub>16–28 Feb</sub> RI <sub>1–15 Mar</sub> , RI <sub>16–31 Mar</sub> RI <sub>1–15 Apr</sub> , RI <sub>16–30 Apr</sub>	<b>DD<sub>1 Nov–15 Apr</sub></b> <b>DTFF<sub>16–30 Apr</sub></b> <b>RI<sub>16–31 Mar</sub></b> RI <sub>16–30 Apr</sub>
1–15 May	DD <sub>1 Nov–30 Apr</sub> DTFF <sub>1–15 May</sub> RI <sub>1–15 Jan</sub> , RI <sub>16–31 Jan</sub> RI <sub>1–15 Feb</sub> , RI <sub>16–28 Feb</sub> RI <sub>1–15 Mar</sub> , RI <sub>16–31 Mar</sub> RI <sub>1–15 Apr</sub> , RI <sub>16–30 Apr</sub> RI <sub>1–15 May</sub>	<b>DD<sub>1 Nov–30 Apr</sub></b> <b>RI<sub>16–31 Mar</sub></b> <b>RI<sub>16–30 Apr</sub></b> RI <sub>1–15 May</sub>
16–31 May	DD <sub>1 Nov–15 May</sub> DTFF <sub>16–31 May</sub> RI <sub>1–15 Jan</sub> , RI <sub>16–31 Jan</sub> RI <sub>1–15 Feb</sub> , RI <sub>16–28 Feb</sub> RI <sub>1–15 Mar</sub> , RI <sub>16–31 Mar</sub> RI <sub>1–15 Apr</sub> RI <sub>16–30 Apr</sub> , RI <sub>1–15 May</sub> RI <sub>16–31 May</sub>	<b>DD<sub>1 Nov–15 May</sub></b> DTFF <sub>16–31 May</sub> RI <sub>16–31 Mar</sub> <b>RI<sub>16–30 Apr</sub></b> <b>RI<sub>1–15 May</sub></b> <b>RI<sub>16–31 May</sub></b>

Parameters in bold were selected as significant by stepwise regression analysis of the original data set.

DD, degree days accumulated up to the trapping interval; DTFF, number of days with temperatures favorable for flight (temperatures above 20 °C); RI, rainfall index. Subscripts denote the time interval for each parameter.

of Worner et al. (2002) and Lankin et al. (2008). The data were re-sampled 30 times in which each location-year was removed from one sample. Stepwise regression was then performed for each of the 30 sets of re-sampled data using the same parameters submitted to stepwise regression in the complete data set.

The bootstrap re-sampling technique utilizes re-sampling of the original data points with replacement. In other words, a re-sampled data set contains the same number of data points as the original data set, but multiple instances of a location-year and absence of other location-years are possible. Ten thousand re-sampled data sets were created and subjected to stepwise regression using the same parameters submitted to the stepwise regression in the

original data set. For both the jackknife and bootstrap analyses, frequency of occurrence of a parameter in all stepwise regressions and 95% confidence intervals for the partial regression coefficients for each parameter estimate are reported.

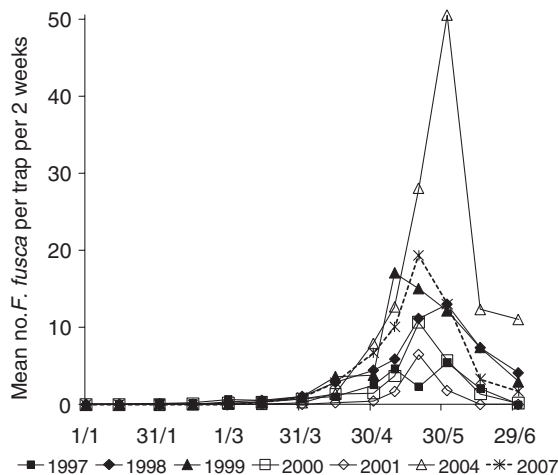
### Results

During spring in North Carolina and Virginia, *F. fusca* dispersal from winter annual hosts typically began to increase during April and peaked during May and early June (Figure 2). However, the timing and magnitude of these dispersal flights varied among years (Figure 2) and among locations within years as illustrated by the data for 2007 (Figure 3).

#### Trapping interval: 1–15 April

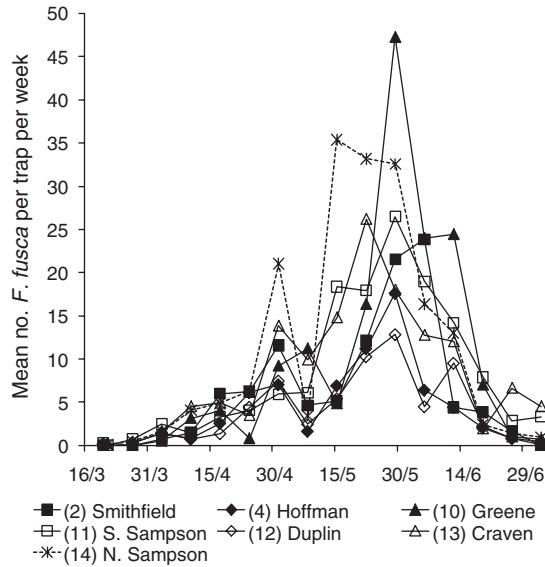
Sixty-two percent of the total variation in the mean number of *F. fusca* adults per location captured between 1 and 15 April each year was explained by a regression model that included DD<sub>1 Nov–31 Mar</sub> and RI<sub>16–31 Mar</sub> (1–2 weeks prior to trapping interval) as independent variables ( $F_{2,27} = 22.32$ ,  $P < 0.01$ ; Table 2). DD<sub>1 Nov–31 Mar</sub> alone accounted for 48% of the total variation while RI<sub>16–31 Mar</sub> explained 15%. The mean number of *F. fusca* adults per location captured between 1 and 15 April was positively related to DD<sub>1 Nov–31 Mar</sub>, but negatively related to late March rainfall.

All stepwise regression models created from jackknife data samples ( $n = 30$ ) contained both DD<sub>1 Nov–31 Mar</sub> and RI<sub>16–31 Mar</sub> parameters (Table 3). In re-sampled data using



**Figure 2** Mean number of *Frankliniella fusca* captured per sampling period over 44 sites in central and eastern North Carolina and Virginia from 1997 to 2001, 2004, and 2007. Values are means across all sites within a year.





**Figure 3** Mean number of *Frankliniella fusca* captured from 20 March–30 June 2007 at seven locations in central and eastern North Carolina and Virginia. Values are means across all sites within a location. Numbers in parentheses correspond to the position on the map in Figure 1. Variation in mean number of *F. fusca* captured in 2007 is representative of the variation among locations within other years (not shown).

bootstrap analysis (n = 10 000), the DD<sub>1 Nov–31 Mar</sub> and RI<sub>16–31 Mar</sub> parameters were selected in 96.8 and 89.2% of models, respectively. Upper and lower 95% confidence

interval values were positive for DD<sub>1 Nov–31 Mar</sub> coefficients and negative for RI<sub>16–31 Mar</sub> coefficients in both jackknife and bootstrap analysis. DTF<sub>1–15 Apr</sub> was not significant in any of the jackknife regression models but was included as a significant variable in 18.8% of the bootstrap models (Table 3).

**Trapping interval: 16–30 April**

Seventy-nine percent of the total variation in the mean number of *F. fusca* adults per location captured between 16 and 30 April was explained by a regression model that included DTF<sub>16–30 Apr</sub> (during the trapping interval), the RI<sub>16–31 Mar</sub> (3–4 weeks prior to the interval), and DD<sub>1 Nov–15 Apr</sub> as independent variables (F<sub>3,26</sub> = 33.48, P < 0.01; Table 2). The partial regression coefficients for all the independent variables were significant at P < 0.02. DTF<sub>16–30 Apr</sub> accounted for 62% of the total variation, indicating that in some locations and years the number of days when temperatures were below the flight threshold was limiting dispersal. RI<sub>16–31 Mar</sub> explained an additional 12%, and DD<sub>1 Nov–15 Apr</sub> explained 5%. The mean number of *F. fusca* adults per location captured between 16 and 30 April was positively related to DTF<sub>16–30 Apr</sub> and DD<sub>1 Nov–15 Apr</sub> but negatively related to RI<sub>16–31 Mar</sub>.

In the jackknife analysis for the 16–30 April trapping interval, 29 of 30 (96.7%) jackknife samples yielded regression models with the same parameters as the original data set (Table 3). One jackknife re-sample model included RI<sub>16–31 Apr</sub> in addition to the parameters chosen for the original data set.

**Table 2** Regression equations and statistics for dispersing *Frankliniella fusca* caught on traps during successive time intervals in spring

Trapping interval	Equation to estimate the number of log-transformed <i>F. fusca</i>	P-value	F-value	d.f.	Model R <sup>2</sup>
1–15 April	$= -1.40 + (0.006)(DD_{1\text{ Nov}-31\text{ Mar}}) - (0.02)(RI_{16-31\text{ Mar}}) + (0.005)$ P-value <0.01 <0.01 Partial R <sup>2</sup> 0.48 0.15	<0.01	22.3	2.27	0.62
16–30 April	$= -1.42 + (0.19)(DTFF_{16-31\text{ Apr}}) - (0.03)(RI_{16-31\text{ Mar}}) + (0.003)(DD_{1\text{ Nov}-15\text{ Apr}})$ P-value <0.01 <0.01 0.02 Partial R <sup>2</sup> 0.62 0.12 0.05	<0.01	33.5	3.26	0.79
1–15 May	$= -0.19 - (0.02)(RI_{16-31\text{ Mar}}) + (0.006)(DD_{1\text{ Nov}-30\text{ Apr}}) - (0.02)(RI_{16-31\text{ Apr}})$ P-value <0.01 <0.01 <0.01 Partial R <sup>2</sup> 0.47 0.18 0.09	<0.01	24.8	3.26	0.74
16–31 May	$= 1.98 - (0.02)(RI_{16-31\text{ May}}) - (0.02)(RI_{16-31\text{ Apr}}) + (0.09)(DD_{1\text{ Nov}-15\text{ May}}) + (0.04)(RI_{1-15\text{ May}})$ P-value <0.01 <0.01 0.02 0.08 Partial R <sup>2</sup> 0.34 0.21 0.09 0.04	<0.01	13.3	4.25	0.68

DD, degree days accumulated up to the trapping interval; DTF, number of days with temperatures favorable for flight (temperatures above 20 °C); RI, rainfall index. Subscripts denote the time interval for each parameter.

**Table 3** Frequency and confidence intervals of parameters in jackknife and bootstrap analyses of stepwise regressions of dispersing populations of *Frankliniella fusca* during successive time intervals in spring related to degree days accumulated up to the trapping interval, rainfall index, and days with temperatures favorable for flight during the trapping interval

Trapping Interval	Regression parameters	% jackknife frequency	95% jackknife confidence interval	% bootstrap frequency	95% bootstrap confidence interval
1–15 April	<b>DD<sub>1 Nov–31 Mar</sub></b>	100.0	0.003 to 0.009	96.8	0.003 to 0.006
	DFFF <sub>1–15 Apr</sub>	0.0	–	18.8	–
	<b>RI<sub>16–31 Mar</sub></b>	100.0	–0.03 to –0.008	89.2	–0.03 to –0.005
	Contains <sup>1</sup> <b>DD<sub>1 Nov–31 Mar</sub></b>	100.0	–	85.9	–
	<b>RI<sub>16–31 Mar</sub></b> Original data model	100.0	–	72.1	–
16–30 April	<b>DD<sub>1 Nov–15 Apr</sub></b>	100.0	–0.001 to 0.005	81.1	–0.0002 to 0.005
	<b>DFFF<sub>16–30 Apr</sub></b>	100.0	0.09 to 0.37	85.5	0.06 to 0.32
	<b>RI<sub>16–31 Mar</sub></b>	100.0	–0.05 to –0.006	96.6	–0.04 to –0.005
	RI <sub>16–31 Apr</sub>	3.3	–	32.2	–
	Contains <sup>1</sup> <b>DD<sub>1 Nov–15 Apr</sub></b> <b>DFFF<sub>16–30 Apr</sub></b> <b>RI<sub>16–31 Mar</sub></b> Original data model	100.0	–	65.5	–
1–15 May	<b>DD<sub>1 Nov–30 Apr</sub></b>	100.0	0.004 to 0.007	93.8	0.003 to 0.008
	<b>RI<sub>16–31 Mar</sub></b>	100.0	–0.03 to –0.007	84.1	–0.04 to 0.003
	<b>RI<sub>16–30 Apr</sub></b>	100.0	–0.03 to –0.008	87.8	–0.04 to –0.003
	RI <sub>1–15 May</sub>	0.0	–	29.3	–
	Contains <sup>1</sup> <b>DD<sub>1 Nov–30 Apr</sub></b> <b>RI<sub>16–31 Mar</sub></b> <b>RI<sub>16–30 Apr</sub></b> Original data model	100.0	–	70.3	–
16–31 May	<b>DD<sub>1 Nov–15 May</sub></b>	100.0	–0.0002 to 0.002	73.0	–0.0007 to 0.003
	DFFF <sub>16–31 May</sub>	0.0	–	32.6	–
	RI <sub>16–31 Mar</sub>	0.0	–	24.4	–
	<b>RI<sub>16–30 Apr</sub></b>	100.0	–0.03 to –0.01	92.1	–0.03 to –0.008
	<b>RI<sub>1–15 May</sub></b>	96.7	–0.007 to 0.02	66.4	–0.01 to 0.03
	<b>RI<sub>16–31 May</sub></b>	100.0	–0.03 to –0.003	77.3	–0.04 to 0.01
	Contains <sup>1</sup> <b>DD<sub>1 Nov–15 May</sub></b> <b>RI<sub>16–31 May</sub></b> <b>RI<sub>16–30 Apr</sub></b> Original data model	96.7	–	33.2	–
		96.7	–	15.7	–

Confidence intervals are not available for parameters not selected by stepwise regression using the original data set. Parameters in bold were selected as significant by stepwise regression analysis of the original data set.

DD, degree days accumulated up to the trapping interval; DFFF, number of days with temperatures favorable for flight (temperatures above 20 °C); RI, rainfall index. Subscripts denote the time interval for each parameter.

<sup>1</sup>Frequencies include models that may contain parameters in addition to the parameters found significant using the complete data set.

In the bootstrap analysis, 96.6% of 10 000 regression models generated from the re-sampled data sets, included RI<sub>16–31 Mar</sub> (Table 3). DD<sub>1 Nov–15 Apr</sub> was included in 81.1% of models, and DFFF<sub>16–30 Apr</sub> was included in 85.5% of models. Of 10 000 re-sampled data sets, 65.5% of models contained the parameters from the original 16–30 April model. Of these models, 1 706 models also contained RI<sub>16–30 Apr</sub>.

Both jackknife and bootstrap upper and lower 95% confidence interval values were positive for the partial regression coefficient for DFFF<sub>16–30 Apr</sub> and negative for the RI<sub>16–31 Mar</sub> partial regression coefficient (Table 3). Upper and lower 95% confidence limits for the DD<sub>1 Nov–15 Apr</sub>

coefficient were positive and negative (Table 3), respectively, but all DD<sub>1 Nov–15 Apr</sub> coefficients for re-sampled data sets were positive.

#### Trapping interval: 1–15 May

Seventy-four percent of the total variation in the mean number of *F. fusca* adults per location captured between 1 and 15 May each year was explained by a regression model that included the independent variables RI<sub>16–31 Mar</sub> (5–6 weeks prior to the trapping interval), DD<sub>1 Nov–30 Apr</sub> and RI<sub>16–30 Apr</sub> (2-week period prior to the trapping interval). The overall regression model was highly significant ( $F_{3,26} = 24.77$ ,  $P < 0.01$ ). The partial regression coefficients

for  $RI_{16-31 \text{ Mar}}$ ,  $DD_{1 \text{ Nov}-30 \text{ Apr}}$  and  $RI_{16-30 \text{ Apr}}$  were significant at  $P < 0.01$  (Table 2).  $RI_{16-31 \text{ Mar}}$  accounted for 47% of the total variation,  $DD_{1 \text{ Nov}-30 \text{ Apr}}$  explained an additional 18%, and  $RI_{16-30 \text{ Apr}}$  explained the final 9%. The mean number of *F. fusca* adults per location captured between 1 and 15 May was positively related to  $DD_{1 \text{ Nov}-30 \text{ Apr}}$  but negatively related to  $RI_{16-31 \text{ Mar}}$  and  $RI_{16-30 \text{ Apr}}$ .

In all 30 re-sampled sets of data, the independent variables selected by the stepwise procedures in jackknife analysis were the same as those selected for the 1–15 May model using the original data set (Table 3). Upper and lower 95% confidence intervals were positive for the  $DD_{1 \text{ Nov}-30 \text{ Apr}}$  coefficient and negative for the  $RI_{16-31 \text{ Mar}}$  and  $RI_{16-30 \text{ Apr}}$  coefficients in jackknife analysis (Table 3). In the bootstrap analysis,  $DD_{1 \text{ Nov}-30 \text{ Apr}}$ ,  $RI_{16-30 \text{ Apr}}$  and  $RI_{16-31 \text{ Mar}}$  were included in 93.8, 87.8, and 84.1% of the 10 000 models, respectively (Table 3). These parameters were selected in the 1–15 May model based on the original data set and all three were included together in 70.3% of models generated from re-sampled data. However, 1 305 of the bootstrap models also included  $RI_{1-15 \text{ May}}$  as an additional independent variable. Bootstrap upper and lower 95% confidence intervals were negative for  $RI_{16-30 \text{ Apr}}$  and positive for  $DD_{1 \text{ Nov}-30 \text{ Apr}}$  coefficients. The upper and lower 95% confidence interval coefficients for  $RI_{16-31 \text{ Mar}}$  were positive and negative, respectively.

#### Trapping interval: 16–31 May

Sixty-eight percent of the total variation in mean number of *F. fusca* adults per location captured between 16 and 31 May each year was collectively explained by a regression model that included as independent variables  $RI_{16-31 \text{ May}}$ , during the trapping interval;  $RI_{16-30 \text{ Apr}}$ , 3–4 weeks prior to the trapping interval;  $DD_{1 \text{ Nov}-15 \text{ May}}$ ; and  $RI_{1-15 \text{ May}}$ , 2 weeks immediately prior to the trapping interval. The overall model ( $F_{4,25} = 13.32$ ,  $P < 0.01$ ) and partial regression coefficients for  $RI_{16-31 \text{ May}}$  and  $RI_{16-30 \text{ Apr}}$  were highly significant ( $P < 0.01$ ); partial regression coefficients for  $DD_{1 \text{ Nov}-15 \text{ May}}$  and  $RI_{1-15 \text{ May}}$  were significant at  $P = 0.02$  and  $0.08$ , respectively (Table 2).  $RI_{16-31 \text{ May}}$  accounted for 34% of the total variation, and  $RI_{16-30 \text{ Apr}}$ ,  $DD_{1 \text{ Nov}-15 \text{ May}}$  and  $RI_{1-15 \text{ May}}$  explained an additional 21, 9, and 4%, respectively. The mean number of *F. fusca* adults per location captured between 16 and 31 May was positively related to  $DD_{1 \text{ Nov}-15 \text{ May}}$  and  $RI_{1-15 \text{ May}}$ , but negatively related to the  $RI_{16-31 \text{ May}}$  and  $RI_{16-30 \text{ Apr}}$ .

In the jackknife analysis, all 30 re-sampled data sets yielded models containing  $RI_{16-31 \text{ May}}$ ,  $RI_{16-30 \text{ Apr}}$ , and  $DD_{1 \text{ Nov}-15 \text{ May}}$ , and 29 models (97%) included  $RI_{1-15 \text{ May}}$  (Table 3). Jackknife 95% upper and lower confidence limits for  $RI_{16-31 \text{ May}}$  and  $RI_{16-30 \text{ Apr}}$  coefficients were negative,

and  $DD_{1 \text{ Nov}-15 \text{ May}}$  and  $RI_{1-15 \text{ May}}$  coefficients had positive upper limits but negative lower limits.

In the bootstrap analysis 3 317 (33%) of the re-sampled data sets resulted in models that included as independent variables  $RI_{16-31 \text{ May}}$ ,  $RI_{16-30 \text{ Apr}}$ ,  $DD_{1 \text{ Nov}-15 \text{ May}}$ , and  $RI_{1-15 \text{ May}}$ . Of these models, only 1 586 (16%) contained only the parameters in the regression model based on the original data set for the 16–31 May trapping interval.  $RI_{16-30 \text{ Apr}}$  was included in 92.1% of bootstrap models (Table 3).  $RI_{16-31 \text{ May}}$ ,  $DD_{1 \text{ Nov}-15 \text{ May}}$ , and  $RI_{1-15 \text{ May}}$  occurred in 77.3, 73.0, and 66.4% of models, respectively. Ninety-five percent upper and lower confidence interval limits are negative for the  $RI_{16-30 \text{ Apr}}$  coefficient, but upper and lower limits are positive and negative, respectively, for the  $RI_{16-31 \text{ May}}$ ,  $DD_{1 \text{ Nov}-15 \text{ May}}$ , and  $RI_{1-15 \text{ May}}$  coefficients (Table 3).

## Discussion

On the basis of previous findings of the effects of precipitation on overwintered populations and dispersal of *F. fusca* (Morsello et al., 2008; Morsello & Kennedy, 2009) and other thrips species (Davidson & Andrewartha, 1948; Dintenfass et al., 1987; Kirk, 1997; Lewis, 1997), we hypothesized that, on a landscape scale, spatial and temporal variation in the number of dispersing *F. fusca* caught on sticky traps during specific trapping intervals in spring would be related to winter and spring temperatures and the timing and amount of rainfall events that suppress thrips populations during specific periods prior to a trapping interval. Because daily temperatures during spring in North Carolina at times remain below the flight threshold (ca. 17–21 °C) for thrips and rainfall can prevent thrips flight (Lewis, 1997), we further hypothesized that temperatures and rainfall during a trapping period would also be related to the number of *F. fusca* caught on traps.

These hypotheses focus on the effects of temperature and rainfall on the patterns of variation in the size of dispersing *F. fusca* populations over time and space that exist on a landscape scale. In selecting our trapping sites, we chose agricultural settings typical of those in which damaging *F. fusca* populations occur. However, we made no effort to account for the influence of biotic factors, including host plant species composition and abundance; nor did we account for differences in agricultural practices or specific crops that were planted in the fields adjacent to our traps. Although local thrips populations can be profoundly affected by these and other local factors, temperature and rainfall determine the suitability of the environment for development and dispersal of thrips populations in a manner that is largely independent of these other factors. The data set that we used to examine



these hypotheses included 30 location-years of data on numbers of *F. fusca* caught on yellow sticky traps from locations spanning a range of ca. 500 km north to south and ca. 260 km east to west. The traps were located around the perimeters of and within crop fields that had not been planted at the time trapping began but were planted to tobacco, cotton, soybean, or tomato during the trapping period.

The models presented here capture the effects of temperature and precipitation on population growth and on the suitability of conditions for flight (Kirk, 1997; Lewis, 1997). Despite site-to-site and year-to-year variation in habitat, agricultural practices and other factors, the results of our regression analyses demonstrate that 62, 79, 74, and 68% of the total variation among locations and years in number of dispersing adult *F. fusca* (Hinds) caught on yellow sticky traps during the intervals 1–15 April, 16–30 April, 1–15 May, and 16–31 May, respectively, can be explained by temperature and rainfall. Our results further demonstrate that specific rainfall parameters of importance vary among trapping intervals and the effects of rainfall during particular periods on dispersing *F. fusca* populations can be manifest over a period of as long as 5–6 weeks after the rainfall occurs.

Temperatures above the developmental threshold for *F. fusca* were quantified as cumulative degree days from the estimated mean midpoint of the fall dispersal flight of *F. fusca* from summer to winter hosts through 1-day prior to the beginning of each trapping interval. Because daily temperatures during fall and winter in the Coastal Plain of North Carolina and Virginia fluctuate above and below the lower *F. fusca* developmental threshold and degree days accumulated at different rates among locations and years, it is not surprising that this parameter was highly significant and positive in the regression models for each of the trapping intervals. Degree days explained 48, 5, 18, and 9% of the variation in number of *F. fusca* trapped during the 1–15 April, 16–30 April, 1–15 May, and 16–31 May trapping intervals, respectively (Table 2). Inclusion of degree days in these models is supported by the results of the jackknife and bootstrap analyses (Table 3) and reflects the important role of temperature in determining development rate of thrips.

Warm temperatures can have both positive and negative effects on thrips population growth and dispersal. During winter and early spring, temperatures are below the developmental threshold of *F. fusca* during most days for at least some part of a day. Therefore, temperature may be a limiting factor in population growth, which affects the number of adult thrips available to disperse. Temperature as a limiting factor on population growth may explain why degree

days from 1 November to 30 March accounted for more variation in mean *F. fusca* per location-year than any other parameter in the 1–15 April model (Table 2). Warm temperatures during late April and May favor continued growth of *F. fusca* populations but also hasten senescence of winter annual host plants, which results in an increase in dispersal followed by a rapid decline despite further degree day accumulation (Morsello et al., 2008). This may explain why the DD parameter explained less total variation in mean number of *F. fusca* trapped per location-year than precipitation or days with temperatures favorable for flight for the 16–30 April, 1–15 May, and 16–31 models (Table 2).

Cumulative degree days prior to the trapping interval directly influence population growth and hence the potential size of the population available to disperse, whereas the number of days with temperatures favorable for flight during a trapping interval can be expected to influence the number of thrips that actually disperse during intervals that include several days in which temperatures remain below the flight threshold. DTFF (i.e., days with maximum temperature > 20 °C) was significant only during the 16–30 April trapping interval (Table 2). During that interval, it was the single best explanatory variable, accounting for 62% of the variation in mean number of *F. fusca* adults per location collected on aerial traps. Inclusion of DTFF in the 16–30 April model was strongly supported by the jackknife analysis in which the stepwise regression models for all 30 of the re-sampled data sets contained this variable. The bootstrap analysis showed that DTFF was significant in 86% of the models and rainfall during the trapping interval was significant in 32% of the models for re-sampled data sets (Table 3). This suggests that at a few locations and/or years, rainfall may have limited dispersal on days in which temperatures were above the flight threshold. The suppressive effect of rainfall on dispersal flights is further supported by the finding that rainfall during the 16–31 May trapping interval accounted for 34% of the variation in the mean number of *F. fusca* caught on traps during the 16–31 May interval (Tables 2 and 3).

The number of days with temperatures favorable for flight during the 1–15 April (mean = 8.0, range 3–15) and 16–30 April (mean = 10.4, range = 2–15) trapping intervals were similar. However, neither days with temperatures favorable for flight nor rainfall during the trapping interval were significant in either the original model or any of the models in the jackknife analyses for the 1–15 April trapping interval (Tables 2 and 3). DTFF was significant in 19% of models in bootstrap analysis; it is likely that during 1–15 April, the thrips populations available to disperse were too low to allow influence of number of days with

temperatures favorable for flight to be strongly supported. During the 1–15 April interval, the mean number of dispersing *F. fusca* adults per location caught on traps was low (mean = 2.4, range = 0.8–9.5) compared to the 16–30 April interval (mean = 6.9, range = <0.1–27.5). During later intervals, 1–15 and 16–31 May, temperatures exceeded the flight threshold on most days. The mean number of *F. fusca* adults per location captured during May was even greater than in April (1–15 May mean = 11.8, range = 0.1–54.0, and 16–31 May mean = 30.6, range = 1.6–138.5) and the explanatory variables included in the models for the 1–15 and 16–31 May trapping intervals are those that affect population growth or the direct effects of rainfall on dispersal rather than the suitability of temperatures for flight.

In the stepwise regression models for each of the trapping intervals, rainfall during specific periods prior to the trapping interval had a strong, negative relationship with the number of *F. fusca* caught. Rainfall occurring prior to 15 March was not significantly related to the dispersal dynamics of *F. fusca*. However, rainfall during 16–31 March exhibited a strong, negative relationship with the mean number of *F. fusca* adults per location caught during the 1–15 and 16–30 April, as well as the 1–15 May trapping intervals (Table 2). Inclusion of 16–31 March rainfall in these models is strongly supported by both jackknife and bootstrap analyses (Table 3). In the jackknife analysis, it was included as a significant, negative, independent variable in all of the jackknife models for each of these intervals. Similarly in the bootstrap analysis, rainfall during 16–31 March was included as a significant, negative variable in 89, 97, and 84% of the bootstrap regression models for the 1–15 April, 16–30 April, and the 1–15 May trapping intervals, respectively. Although 16–31 March rainfall was not found to be a significant parameter in the 16–31 May model using the original data set, it was selected in 24% of bootstrap models. Because late March rainfall occurred weeks prior to the 1–15 and 16–30 April and 1–15 May adult trapping intervals, its inclusion in these models undoubtedly reflects the lasting consequences of rainfall-mediated mortality during late March on subsequent population growth and the number of adult thrips available to disperse weeks later (Kirk, 1997; Morsello & Kennedy, 2009). Similarly, rainfall during 16–30 April exerted a lasting negative effect on the *F. fusca* populations, as indicated by its significant relationship with numbers of dispersing *F. fusca* caught during the 1–15 May and 16–31 May trapping intervals (Tables 2 and 3). In contrast, rainfall during 1–15 May was positively related to the number of *F. fusca* captured during the 16–31 May trapping interval. Considerable rainfall in early May delays senescence of winter annual plants that serve as important hosts for *F. fusca* in

spring and allows continued population growth resulting in greater numbers of adults available to disperse in late May.

Using regression analysis, Morsello et al. (2008) found that the majority of variation in total numbers of dispersing *F. fusca* adults caught on sticky traps in spring between 1 April and 31 May can be explained by temperature, amount of precipitation and number of days with precipitation between 1 January and 31 May. Their work did not address changes in the effects of temperature and precipitation on dispersing *F. fusca* populations as the season progressed. Morsello & Kennedy (2009) subsequently demonstrated that the degree to which growth of local *F. fusca* populations on their overwintering host plants in late winter and spring was suppressed by precipitation depended on the timing, amount, and duration of precipitation events, with rainfall during specific periods having a disproportionate effect on local population growth. The results presented herein focus on whether and to what extent the effects of temperature and rainfall on population growth of *F. fusca* at the local level reported by Morsello & Kennedy (2009) can be observed as changes in populations of dispersing adults at the landscape level. Our results extend the previous work by providing strong evidence that the population suppressive effects of precipitation on *F. fusca* population growth reported by Morsello & Kennedy (2009) are subsequently manifest at a landscape scale as reductions in the populations of dispersing adults and that these reductions persist for as long as 5–6 weeks after the precipitation occurs. Moreover, they extend the findings of Morsello et al. (2008) by demonstrating that the within season dynamics of dispersing populations are profoundly influenced by temperature and precipitation patterns, by characterizing the ways in which the influence of temperature and precipitation on dispersing populations of *F. fusca* change as the season progresses, and by providing quantitative estimates of these changes.

Because *F. fusca* is the principal, early-season vector of TSWV in portions of the southeastern USA and incidence of TSWV has been negatively associated with high levels of rainfall during March, our findings have implications for better understanding the epidemiology of TSWV in those areas where *F. fusca* is an important vector (Brown et al., 2005; Olatinwo et al., 2008). From a pest management perspective, our results suggest that, with refinement, weather-based models of the type presented may have value in predicting when area-wide conditions are highly favorable or unfavorable for the development of large *F. fusca* populations during various intervals of importance in spring. However, it is likely that without additional location-specific information, weather-based

models will be of limited value for predicting infestation levels in individual crop fields.

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