Seasonal Dispersal Patterns of *Frankliniella fusca* (Thysanoptera: Thripidae) and Tomato Spotted Wilt Virus Occurrence in Central and Eastern North Carolina

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ABSTRACT The seasonal abundance and temporal pattern of *Frankliniella fusca* Hinds dispersal were monitored from 1996 to 2000 at 12 locations in central and eastern North Carolina. The predominant vector species of tomato spotted wilt virus (TSWV) captured across all locations was *F. fusca* (98%). The temporal patterns of *F. fusca* dispersal observed during spring seasons varied among locations in all years except 2000. Regression analysis estimated that times of first flight in the spring seasons varied among locations, whereas flight duration intervals were similar. Temporal patterns of *F. fusca* captured varied significantly between aerial traps placed 0.1 and 1.0 m above the soil surface. Fewer total thrips were captured at 0.1 m, although thrips dispersal occurred earlier and over a greater time interval compared with 1.0-m traps. Temporal patterns of TSWV occurrence differed among locations in the spring seasons of 1999 and 2000, whereas patterns of virus occurrence were similar during the fall seasons. Patterns of *F. fusca* dispersal and subsequent TSWV occurrence were synchronous at locations in 1999 and 2000 where the greatest number of TSWV lesions was recorded. Knowledge of the temporal patterns of *F. fusca* dispersal and TSWV occurrence may be a useful indicator for describing the time when susceptible crops are at highest risk of TSWV infection.

KEY WORDS *Frankliniella occidentalis*, thrips, tomato spotted wilt virus

TOMATO SPOTTED WILT VIRUS (TSWV) (family Bunyaviridae) occurs annually in most agricultural areas of the southeastern United States and commonly reaches damaging levels in tomato, pepper, peanut, and tobacco (Cho et al. 1995a, Gitaitis et al. 1998, McPherson et al. 1999, Garcia et al. 2000). This virus, which is vectored by at least eight species of thrips (Mound 1996), can be transmitted only by adult thrips that have acquired the virus as larvae from an infected host plant. For a plant to serve as a source for spread of TSWV, it must be susceptible to systemic infection by TSWV and support reproducing populations of vector species (Ullman et al. 1993, Bautista et al. 1996). In the southeast, the tobacco thrips, *Frankliniella fusca* (Hinds), is considered the principal vector (McPherson et al. 1992, Barbour and Brandenburg 1994, Cho et al. 1995a, Johnson et al. 1995, Eckel et al. 1996, Groves et al. 2001a, 2001b), although the western flower thrips, *Frankliniella occidentalis* Pergande, may be important where it is locally abundant (Eckel et al. 1996). The onion thrips, *Thrips tabaci* Lindeman, regularly occurs in this region, but recent studies have indicated that most populations are not competent vectors of TSWV (Wijkamp et al. 1995).

Temporally, thrips populations peak in mid to late spring on newly transplanted crops (Eckel et al. 1996, Gitaitis et al. 1998). Over a 6-year period in Georgia, McPherson et al. (1992) reported that peak densities of *F. fusca*, *F. occidentalis*, and *Frankliniella bispinosa* (Morgan) inhabiting foliage and blossoms of flue-cured tobacco occurred from 3 to 24 May. In South Carolina, thrips populations collected from wheat, cotton, and some wild hosts peaked over a similar interval in May, and included both *F. fusca* and *F. occidentalis* (DuRant et al. 1994). Thrips surveys in North Carolina tobacco, tomato, and pepper documented peak population densities of *F. fusca*, *F. occidentalis*, and *T. tabaci* occurring from mid-May through early June (Eckel et al. 1996).

Populations of viruliferous thrips that disperse into crops in late spring most likely develop on nearby weed hosts (Duffus, 1971; Stewart et al. 1989; Chellemi et al. 1994; Cho et al. 1995a; Johnson et al. 1995; Toapanta et al. 1996; Groves et al. 2001a, 2001b). An understanding of the seasonal dynamics of thrips populations developing on and emigrating from wild hosts is essential to understanding the epidemiology of TSWV. Although the seasonal dynamics of vector species have been described on crop plants (Barbour and Brandenburg 1994, Chamberlin et al. 1992, McPherson

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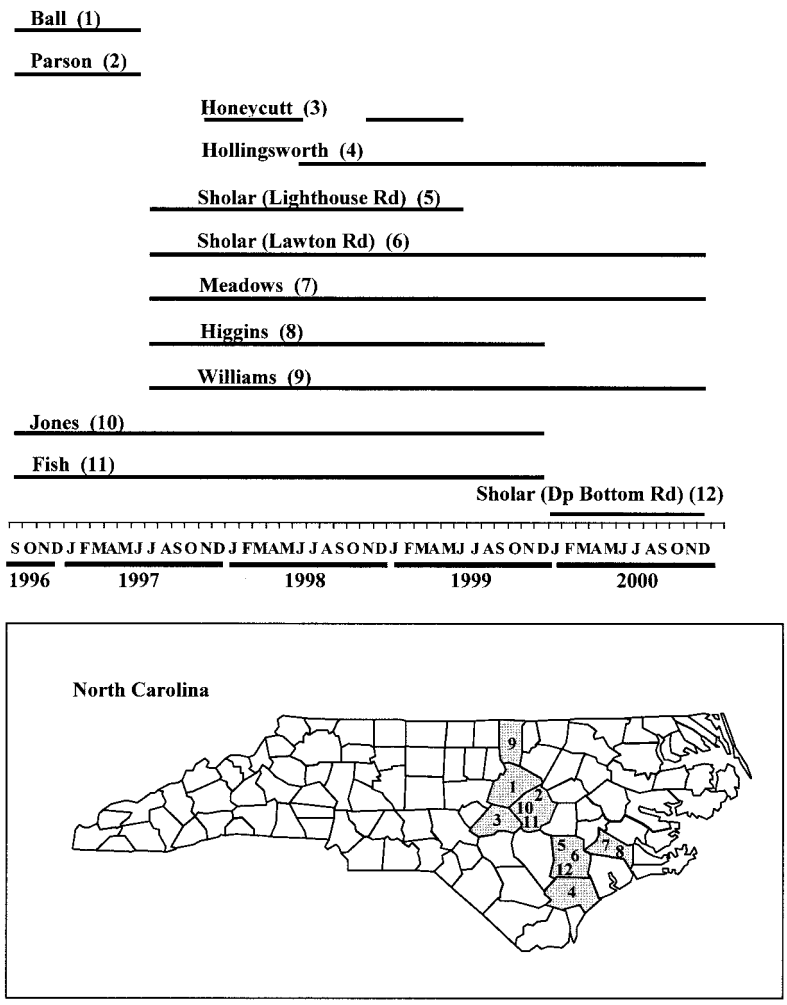

Fig. 1. Aerial trap collection intervals and locations of the 12 sample sites in central and eastern North Carolina where thrips dispersal was recorded.

et al. 1992, Puche et al. 1995, McPherson et al. 1999), information on the seasonal abundance of thrips emigrating from weed hosts is limited. This study was conducted to document the seasonal patterns of thrips dispersal from weeds and to further characterize the temporal patterns of primary spread of TSWV.

Materials and Methods

Aerial Sticky Trap Collection. From 18 September 1996 to 14 November 2000, thrips dispersal was monitored in field borders at 12 locations in central and eastern North Carolina (Fig. 1). Each trap consisted of a cylindrical yellow PVC pipe (7.5 cm length × 2.5 cm diameter) wrapped with Tanglefoot-coated plastic wrap (Great Lakes integrated pest management (IPM), Vestaburg, MI), and fastened to a wooden dowel 1 m above the soil. At each field location, four traps, separated by 10 m, were arranged in a linear pattern along field borders or within noncultivated fields adjacent to sites with a history of TSWV infection. Traps were replaced at ≈14-d intervals, and recovered traps were returned to the laboratory where the coated plastic wrap was removed from the PVC cylinder and sandwiched between two pieces of transparent plastic wrap (S.C. Johnson and Son, Inc., Racine, WI). All sticky traps were then labeled and held at 0°C until thrips could be counted and identified.

Aerial Trap Height. The effect of trap height on thrips capture was investigated from 18 September 1996 to 23 June 1997 at one location in Wake County (Fig. 1, location 1) and three locations in Johnston County (locations 2, 10, and 11), NC. At each of the locations, four trap stands were placed 10 m apart in a linear pattern, and each stand contained two traps suspended 0.1 and 1 m above the soil. Traps were collected and replaced at ≈14-d intervals and adult thrips species counted and identified as described previously.

Thrips Identification. When 25 or fewer adult thrips per trap were collected, all thrips were identified to

species. When more than 25 thrips per trap were captured, a subsample of 25 randomly selected thrips were removed and identified. Individual thrips recovered for identification were removed from the plastic wrap by soaking in HistoClear solvent (National Diagnostics, Atlanta, GA) for 10 min. A microscope slide was prepared for each trap collection (≤25 thrips per slide) using CMC-10 (Masters Chemical Co., Elk Grove, IL) as a clearing and mounting medium. Species of adult thrips mounted on slides were determined using a key to adult thrips of the Terebrantia suborder (Palmer et al. 1992).

Monitoring Occurrence of TSWV. Temporal patterns of TSWV occurrence were monitored in 1998 at locations in Duplin County (Fig. 1, location 5), Granville County (location 9), and Jones County (location 7), NC, from 17 March to 27 July. In 1999, virus occurrence was monitored at different locations in Jones County (location 8), Duplin County (location 6), and Pender County (location 4), NC, from 3 March to 3 December, and in 2000 at the same three locations as those in 1999 plus the Jones County (location 7) and a Duplin County (location 12) location from 27 February to 2 December.

Petunia hybrida variety 'Celebrity Blue' was used as an indicator plant to detect occurrence of TSWV. Plants will begin to show a local lesion in 24–72 h in response to the feeding by an infective thrips. Lesions appear as small brown or black necrotic spots on leaves and result from the hypersensitive response of the petunia plant, which is the plant's strategy to limit systemic infection by the virus. The regular placement and removal of petunia plants gives an indication of when infective vectors are moving into an area by the appearance of a local lesion on petunia after feeding by a viruliferous thrips. However, this technique does not provide accurate information necessary to quantify the intensity of viruliferous thrips feeding given that a single individual may feed at multiple sites resulting in multiple lesions.

Three- to five-week-old greenhouse-grown *P. hybrida* were transplanted in eight groups (four plants per group) in a linear pattern alongside aerial traps at each location. Each group of four plants was planted into a 1 m^2 area of bare soil and separated by 10 m (total 32 plants/location). All plants were collected and replaced with 3- to 5-week-old plants every 7–10 d. Flowers were removed from plants immediately before transplanting because they are attractive to many thrips species and flower petals do not appear to express local lesions (Ullman et al. 1998).

Petunia hybrida plants were returned to the laboratory and placed in a greenhouse for 48 h to allow TSWV lesions to form on recently inoculated leaves. After 48 h, all leaves were visually examined for suspected TSWV lesions (Wijkamp and Peters 1993). Each lesion was removed and confirmed positive for TSWV using double antibody sandwich, enzyme-linked immunosorbent assay (DAS-ELISA) (Agdia, Inc., Elkhart, ID). Assays were scored on a THERMOmax microtiter plate reader (Molecular Devices Corp., Menlo Park, CA) at a transmission wavelength of 405 nm. Samples were considered positive for TSWV if the optical density exceeded the mean plus three standard deviations above uninfected controls.

Data Analysis. Because thrips populations increased rapidly in late spring, declined, and then peaked again in late summer to early fall, trap capture data were divided into a spring (1 January through 15 July) and a fall (16 July through 31 December) interval for each year. For each data set, thrips populations were expressed as the proportion captured per trap per location, season, and year. When 25 or more *F. fusca* were captured per season, mean seasonal proportions were arcsine transformed and subjected to repeated measures analysis of variance (ANOVA) to compare means among locations. Regression estimates of first flight date (T_0) and the median time interval (days) over which the middle 50% of thrips were captured (T_{25}–T_{75}) within a season were determined by regressing logit-transformed mean *F. fusca* proportions on Julian date. Comparisons among locations of both regression estimates were conducted using ANOVA. When fewer than 25 *F. fusca* were captured in a single season per location, or when regression correlation coefficients were <0.90, no regression estimate comparisons were conducted. Mean proportion data, collected from two trap heights (0.1 and 1 m), were log transformed and analyzed using ANOVA. Regression estimates of T_0 and T_{25}–T_{75}, derived from the empirical logit transformation, were compared between trap heights.

The number of DAS-ELISA confirmed TSWV lesions recorded from *P. hybrida* were represented as the mean proportion of lesions detected for each location, season, and year. Proportion data were arcsine transformed and subjected to a repeated measures ANOVA to compare patterns of TSWV occurrence among locations over time when 25 or more confirmed TSWV lesions were recorded per season and location. Regression estimates (T_0 and T_{25}–T_{75}) were also determined by regressing logit-transformed cumulative proportion of lesions on Julian date. Regression estimates were not compared among locations when fewer than 25 confirmed TSWV lesions were recorded in a season or where regression correlation coefficients were <0.90. All statistical tests described were conducted using SAS (SAS Institute 1998).

Results

Aerial Trap Collection. Over the 52-mo experiment across 12 locations, an estimated 76,364 adult thrips were captured on aerial sticky traps. Approximately 7% (n = 5,237) of the adult thrips captured represented species previously reported as capable of transmitting TSWV. Adult *F. fusca* was the predominant TSWV-vector species, comprising >98% (n = 5,139) of total vectors followed by adult *F. occidentalis*, which comprised ≈2% (n = 98) (Fig. 2). A substantial number of *T. tabaci* were also collected (n = 1,400), but the ability of this species to transmit the predominant TSWV isolates occurring in the southeastern United

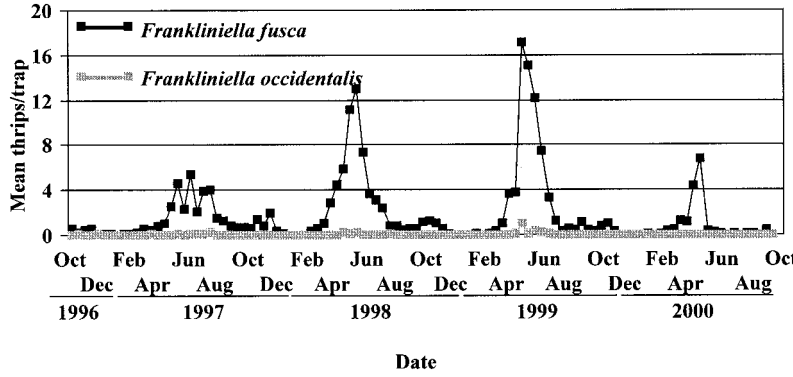

Fig. 2. Mean number of *F. fusca* and *F. occidentalis* captured per trap averaged over 12 field locations in eastern North Carolina from the fall of 1996 through the fall of 2000.

States is currently unknown. Collectively, flower thrips, *Frankliniella tritici* (Fitch), grain thrips, *Limothrips cerealium* (Haliday), and soybean thrips, *Neohydatothrips variabilis* (Beach), accounted for >70% (n = 53,551) of nonvector species captured. Because *F. fusca* was the dominant TSWV vector species captured in this study, the remaining results focus on this species.

Seasonal patterns of *F. fusca* dispersal, expressed as mean proportions of *F. fusca* captured on aerial traps, varied among locations in three out of four spring seasons (Fig. 3A–D). Specifically, mean proportions significantly varied among locations in the spring seasons of 1997, 1998, and 1999 (F = 1.81, df = 36,108, P = 0.01; F = 2.55, df = 14,42, $P < 0.0001$; F = 3.08, df = 96,288, $P < 0.0001$, respectively), but they did not differ in 2000 (F = 0.99, df = 92,276, P = 0.52). Patterns of *F. fusca* dispersal also differed among locations in the fall seasons of 1997 and 1998 (Fig. 3E–F) (F = 4.33, df = 12,36, P = 0.0003; F = 2.55, df = 14,42, P = 0.01, respectively). Statistical analysis of mean proportions of *F. fusca* captured in the fall seasons of 1999 and 2000 were not conducted because of the low numbers of adult *F. fusca* captured.

In an effort to assess the time(s) in early spring when adult *F. fusca* began to disperse from overwintering hosts and potentially initiate TSWV transmission from overwintering inoculum sources, the date of first *F. fusca* capture (T_0) was estimated by regressing logit-transformed mean proportions on Julian date. Estimated T_0 dates varied significantly among locations in each of the four spring seasons surveyed from 1997 to 2000 (F = 11.65, df = 3,11, P = 0.0002; F = 5.54, df = 5,18, P = 0.01; F = 9.87, df = 4,15, $P < 0.0001$; F = 9.11, df = 4,15, P = 0.0004, respectively) (Table 1). In spring 1997, estimated first adult *F. fusca* capture ranged from 12 January to 16 March among the four locations sampled, from 9 March to 9 April among six locations sampled in 1998, from 16 March to 16 April among five locations in 1999, and from 27 February to 22 March among five locations in 2000.

To characterize the time interval(s) during which the greatest number of *F. fusca* were captured (and the risk for TSWV transmission potential was greatest), the median flight interval containing the middle 50% of *F. fusca* (T_{25}–T_{75}) was estimated using logit regression of mean proportions captured versus Julian date. In the spring season of 1997, estimated T_{25}–T_{75} intervals significantly differed among the four locations (F = 8.16, df = 3,11, P = 0.004), ranging from 32 to 62 d. However, T_{25}–T_{75} intervals did not differ among the locations in spring seasons of 1998, 1999, and 2000 (F = 0.75, df = 5,18, P = 0.39; F = 0.91, df = 4,15, P = 0.48; F = 0.92, df = 4,15, P = 0.75, respectively), with the mean duration of these median flight intervals averaging 28, 25, and 29 d, respectively. In addition, T_{25}–T_{75} values for the fall seasons of 1997 and 1998 did not significantly differ among locations (F = 1.13, df = 2,6, P = 0.33; F = 0.56, df = 2,6, P = 0.5982, respectively), with the estimated intervals averaging 19 and 20 d, respectively. Again, low numbers of *F. fusca* prohibited comparisons among locations of regression estimated T_{25}–T_{75} values in the fall seasons of 1999 and 2000.

Aerial Trap Height. Temporal patterns of *F. fusca* dispersal differed significantly on traps at heights of 0.1 versus 1.0 m at field location 11 (Fig. 1) (F = 2.14, df = 13,39, P = 0.04), 2 (F = 5.48, df = 13,39, $P < 0.0001$), and 10 (F = 3.59, df = 13,39, P = 0.001) in the spring of 1997 (Figs. 4B–D, respectively), whereas no significant differences were observed at location 1 (F = 2.92, df = 1,3, P = 0.19) (Fig. 4A). Regression estimates of first *F. fusca* flight (T_0) significantly differed between the two trap heights at locations 1, 11, 10, and 2 (F = 29.76, df = 1,6, $P < 0.0001$; F = 14.46, df =1, 6, P = 0.0009; F = 27.51, df =1,6, $P < 0.0001$; F = 39.14, df = 1,6, $P < 0.0001$, respectively) (Table 2). In each case, a negative T_0 value was estimated for the lower trap height, indicating that dispersal was ongoing before the first sample date of the spring season. Estimated T_{25}–T_{75} values also significantly differed between trap heights at each of the four locations 1, 11, 10, and 2 (F = 6.57, df = 1,6, P = 0.048; F = 13.16, df = 1,6, P = 0.0006; F = 8.60, df = 1,6, P = 0.03; F = 11.35, df = 1,6, P = 0.02, respectively). Because of the low number of thrips captured during the fall, 1996 season,

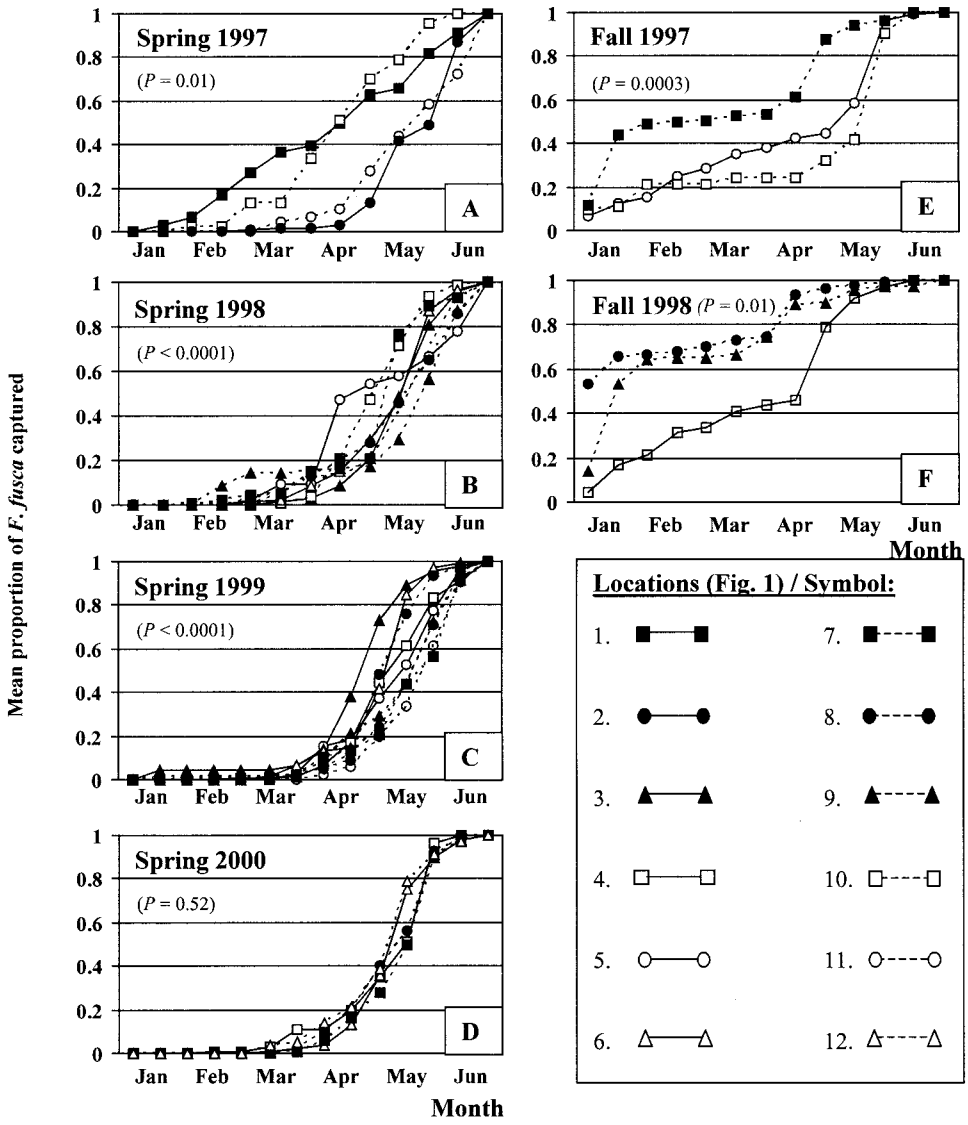

Fig. 3. Mean seasonal proportions of *F. fusca* captured on aerial traps from fall 1996 through fall 2000. Probabilities of differences in mean proportions of adult *F. fusca* captured among locations are provided ($\alpha = 0.05$).

regression estimates of T_0 and T_{25}–T_{75} values were not compared.

TSWV Occurrence. Among the three locations sampled in 1998, no DAS-ELISA confirmed TSWV lesions were recorded from *P. hybrida* plants. In 1999, a total of 69 confirmed TSWV lesions were recorded from *P. hybrida*, with the majority ($n = 58$) recovered from plants placed at location 8 (Fig. 1) and the remainder from location 4 ($n = 11$). No confirmed TSWV lesions were recorded from *P. hybrida* plants at location 6. At four of the five locations sampled in 2000, a total of 98 confirmed TSWV lesions were recorded, with the majority ($n = 58$) collected from location 12 and relatively equal numbers collected from locations 4 ($n = 15$), 6 ($n = 13$), and 8 ($n = 12$). In 2000, no confirmed TSWV lesions were found on *P. hybrida* plants at location 7.

Temporal patterns of *F. fusca* dispersal and TSWV occurrence were similar in the spring season of 1999 at location 8 ($F = 3.10$, df = 1,3, $P = 0.40$) and at location 12 in 2000 ($F = 0.48$, df = 17,51, $P = 0.95$), the locations where the majority of confirmed TSWV lesions were recorded. In the subsequent fall seasons of 1999 and 2000, patterns of *F. fusca* dispersal and TSWV occurrence were similar at all locations sampled where TSWV lesions were detected, except for field location 8 ($F = 32.58$, df = 1,3, $P = 0.01$). Specifically, patterns of vector movement and virus spread in the fall seasons were similar at location 4 in 1999 ($F = 0.31$, df = 1,3, $P = 0.6323$), and at locations

Table 1. Sample attributes of twelve populations of *F. fusca* collected on aerial sticky traps based on the mean cumulative proportions captured in eastern North Carolina

Year	Season	Field	*n*	Regression parameters Logits vs Time	Regression estimates[a]		
					r^2	T_0	T_{25}–T_{75}
1997	Spring	Ball	36	$-3.82 + 0.04\,x_i$	0.96	12a	62a
		Fish	37	$-7.55 + 0.06\,x_i$	0.98	47b	35b
		Jones	45	$-6.09 + 0.06\,x_i$	0.97	25a	37b
		Parson	205	$-9.65 + 0.07\,x_i$	0.93	75c	32b
	Fall	Jones	26	$-43.11 + 0.14\,x_i$	0.93	–[b]	16a
		Meadows	43	$-33.60 + 0.11\,x_i$	0.92	–	20a
		Sholar (Light)	72	$-30.81 + 0.10\,x_i$	0.91	–	22a
1998	Spring	Higgins	424	$-10.77 + 0.07\,x_i$	0.98	83ab	30a
		Honeycutt	124	$-14.69 + 0.10\,x_i$	0.96	99a	22a
		Jones	249	$-12.38 + 0.09\,x_i$	0.90	85ab	24a
		Meadows	144	$-9.46 + 0.07\,x_i$	0.92	69b	31a
		Sholar (Lawton)	434	$-11.99 + 0.09\,x_i$	0.97	85ab	25a
		Sholar (Light)	69	$-8.72 + 0.06\,x_i$	0.93	68b	36a
	Fall	Higgins	49	$-27.70 + 0.09\,x_i$	0.96	–	24a
		Hollingsworth	27	$-24.16 + 0.08\,x_i$	0.93	–	17a
		Williams	25	$-21.48 + 0.07\,x_i$	0.91	–	18a
1999	Spring	Fish	151	$-16.52 + 0.11\,x_i$	0.96	106a	20a
		Hollingsworth	576	$-11.02 + 0.08\,x_i$	0.98	79b	27a
		Meadows	114	$-10.80 + 0.08\,x_i$	0.91	83b	29a
		Sholar (Lawton)	377	$-11.67 + 0.09\,x_i$	0.92	75b	23a
		Sholar (Light)	283	$-10.90 + 0.08\,x_i$	0.91	78b	27a
2000	Spring	Higgins	41	$-10.85 + 0.08\,x_i$	0.98	75ab	27a
		Hollingsworth	81	$-8.37 + 0.07\,x_i$	0.92	68b	34a
		Meadows	100	$-11.28 + 0.08\,x_i$	0.97	81a	27a
		Sholar (Deep Bot)	85	$-8.85 + 0.07\,x_i$	0.98	69b	31a
		Sholar (Lawton)	83	$-11.36 + 0.09\,x_i$	0.97	79a	26a

[a] Mean regression estimates not followed by the same letter within columns by year and season are significantly different by PROC GLM, LSMEANS ($\alpha = 0.05$).

[b] First flight regression estimates not determined for summer/fall seasons.

8, 12, and 6 in 2000 ($F = 1.33$, df = 18,54, $P = 0.34$; $F = 1.70$, df = 18,54, $P = 0.07$; $F = 0.74$, df = 18,54, $P = 0.76$, respectively).

Discussion

In this study, two potential TSWV thrips vector species, *F. fusca* and *F. occidentalis*, were captured on aerial traps at the 12 locations surveyed. In total, very few *F. occidentalis* were captured at any of the sample sites in central and eastern North Carolina. These findings are consistent with Eckel et al. (1996), who reported that populations of *F. occidentalis* occurred infrequently in eastern and central parts of the state and were only locally abundant in tomato and pepper crops in the west. As a result, *F. fusca* appears to be the species presently responsible for vectoring TSWV from weed species to susceptible crops in central and eastern North Carolina.

Frankliniella fusca is highly polyphagous, feeding and reproducing on a variety of grasses (Newsom et al. 1953, Toapanta et al. 1996), broadleaf weeds (Beckham et al. 1971; Stewart et al. 1989; Cho et al. 1995b; Groves et al. 2001a, 2001b), and cultivated crops (Newsom et al. 1953, Salguero Navas et al. 1991, Chamberlin et al. 1992, Eckel et al. 1996, Toapanta et al. 1996). Many macropterous adult thrips make short-distance dispersal flights away from maturing, overwintering hosts in the spring season when environmental conditions are conducive to flight (Cho et al. 1989, Lewis 1997, Groves et al. 2001a), and there is strong evidence to suggest that dispersing thrips originate from wild plant species occurring along field margins or in noncultivated areas near crops (Bond et al. 1983; Chamberlin et al. 1992; Chellemi et al. 1994; Toapanta et al. 1996; Groves et al. 2001a, 2001b). Moreover, TSWV has been documented to infect a large number of plant species across a broad range of plant families and plant types, including herbaceous annuals, biennials, and perennials (Bond et al. 1983; Cho et al. 1986; Cho et al. 1987; Stobbs et al. 1992; Kaminska and Korbin 1994; Johnson et al. 1995; Jorda et al. 1995; Latham and Jones 1997; Gitaitis et al. 1998; Groves et al. 2001a, 2001b). Variation in the distribution, abundance, and seasonal maturation of these different weed species concomitantly harboring TSWV infections and reproducing populations of *F. fusca* likely contributed to the observed differences in temporal patterns and estimated times of first movement (T_0) of vectors and virus spread among locations during the four spring seasons. Similarly, the temporal patterns of TSWV occurrence, as measured by confirmed TSWV lesions recorded from *P. hybrida*, varied among locations sampled in the spring seasons. Variation among plant species in distribution, abundance, and seasonal maturation, concomitantly harboring reproducing populations of *F. fusca*, likely influenced the observed timing and duration of TSWV spread.

Although the overall patterns of *F. fusca* dispersal and estimated date of first capture (T_0) differed

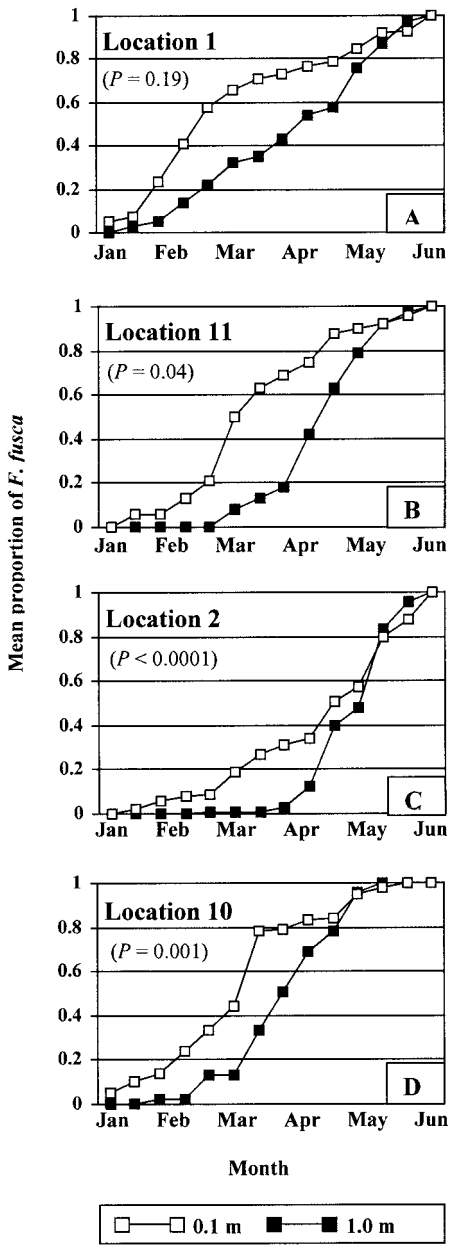

Fig. 4. Mean proportions of *F. fusca* captured on traps placed 0.1 and 1.0 m above the soil surface at four field locations in the spring season, 1997. Probabilities of a difference in proportions of *F. fusca* captured between trap heights are provided ($\alpha = 0.05$).

among locations surveyed in three of the four spring seasons of this study, the estimated time intervals encompassing the middle 50% of dispersing *F. fusca* (T_{25}–T_{75}) were similar among locations, except in 1997 when only a single location (Fig. 1, location 1) had a protracted interval. In the spring seasons of 1998–2000, the duration of these estimated T_{25}–T_{75} intervals averaged 28, 25, and 29 d, respectively. In 1998, the T_{25}–T_{75} interval was centered on Julian day 140 (20 May), ranging between 6 May and 3 June. In 1999, the estimated interval was centered on Julian day 137 (17 May), and ranged between 4 May and 30 May; whereas in 2000, the estimated central Julian day was 130 (10 May) and ranged between 25 April and 25 May.

In many susceptible crops planted in central and eastern North Carolina, TSWV symptom expression begins in early June. Doraiswamy et al. (1984) reported that systemic symptoms in 79 plant species occurred 15–25 d after inoculation under glasshouse conditions held at 28°C. Assuming a comparable latency period in susceptible, field-grown crops growing in the late spring, the onset of TSWV spread in North Carolina would be predicted to occur beginning in mid and lasting through late May. Our results indicate that the estimated peak interval of *F. fusca* dispersal flights (T_{25}–T_{75}) coincided with this proposed period of TSWV spread in three of the four years of this study.

In the fall seasons of this study, overall patterns of *F. fusca* dispersal were less variable among locations compared with the spring seasons. In both 1997 and 1998, the estimated T_{25}–T_{75} intervals varied by only 6 d among the locations sampled, with an average median flight date occurring on day 309 (5 November) in 1997 and 299 (26 October) in 1998. Furthermore, the estimated T_{25}–T_{75} interval averaged 19 d in 1997 (26 October to 15 November) and 20 d in 1998 (16 October to 5 November). The observed synchrony in the overall patterns of fall flights and estimated median flight intervals was closely associated with the first hard freeze date of the fall season, which occurred on 30 October in 1997 and 25 October in 1998 (SCO 1997, 1998, Willard 4 SW, NC). These first freeze dates preceded the midpoint of the rather short duration dispersal flights by only five and 2 d in 1997 and 1998, respectively, perhaps forcing thrips to disperse from maturing summer annual and perennial weeds onto other perennial or newly germinated winter annual weed species. Likewise, patterns of virus spread were similar among locations in the fall seasons of 1999 and 2000. In the fall of 1999, TSWV-infected lesions were recovered on only two consecutive collection dates; day 291 (18 October) and 305 (1 November) with the first fall freeze date in 1999 occurring in the middle of this 2-wk interval at day 298 (25 October) (SCO 1999, Willard 4 SW, NC). Again in 2000, nearly all of the TSWV spread in the fall season occurred over a 2-wk interval between day 283 (10 October) and 297 (24 October) with the first fall freeze on 10 October (SCO 2000, Willard 4 SW, NC). This fall dispersal of vectors provides a means by which TSWV can spread from declining summer hosts to overwintering winter annual or perennial weed species (Groves et al. 2001a, 2001b).

The height at which aerial traps were placed above the soil impacted the observed pattern of *F. fusca* capture. Specifically, dispersal of *F. fusca* among weed hosts occurred earlier on 0.1 versus 1.0 m height traps. Negative first flight date estimates (T_0) at 0.1 m suggests that *F. fusca* were dispersing before trapping was

Table 2. Sample attributes of four field populations of *F. fusca* collected on aerial sticky traps at two heights above the soil surface (0.1 and 1.0 m) based on the mean proportions captured

Year	Season	Field	Trap ht (m)	*n*	Regression parameters Logits vs Time	Regression estimates[a]		
						r^2	T_0	T_{25}–T_{75}
1997	Spring	Ball	0.1	84	$-2.35 + 0.03\,x_i$	0.90	−14a	88a
			1.0	36	$-3.82 + 0.04\,x_i$	0.96	12b	62b
		Fish	0.1	48	$-3.57 + 0.04\,x_i$	0.97	−26a	65a
			1.0	37	$-7.55 + 0.06\,x_i$	0.98	47b	35b
		Jones	0.1	63	$-3.23 + 0.04\,x_i$	0.97	−32a	61a
			1.0	45	$-6.09 + 0.06\,x_i$	0.97	25b	37b
		Parson	0.1	128	$-4.22 + 0.03\,x_i$	0.98	−11a	76a
			1.0	205	$-9.65 + 0.07\,x_i$	0.93	75b	32b

[a] Mean regression estimates not followed by the same letter within columns by field location are significantly different by PROC GLM, LSMEANS ($\alpha = 0.05$).

initiated in January 1997. Additionally, the median flight interval during which 50% of *F. fusca* were captured (T_{25}–T_{75}) in the spring season was also significantly more protracted at 0.1 versus 1.0 m. Although fewer thrips were captured at the lower trap height, they dispersed earlier and over a much longer period of time. In addition, all of the adult *F. fusca* captured at both trap heights in this portion of the study were of the macropterous wingform. Many of the thrips captured at 0.1 m through the winter and early spring period were probably engaged in only very short distance dispersal. Such dispersal may enhance the opportunity for localized spread of TSWV from nearby overwintering hosts to adjacent, noninfected plant species, contributing to a rapid, localized build-up of inoculum before susceptible crops are planted. Groves et al. (2001a) observed such a phenomenon, where there was considerable spread of TSWV from chickweed to small flower buttercup in the early spring before susceptible crops were planted and when tobacco thrips populations were rapidly increasing.

Because vector control using insecticides is of limited effectiveness in reducing spread of TSWV into susceptible crops (Funderburk et al. 1990, Todd et al. 1996) and commercially acceptable TSWV-resistant varieties are not yet available, successful long-term management of TSWV may require the ability to recognize those periods or intervals of high risk for transmission of TSWV. Depicted in Fig. 5A is a conceptual model illustrating the potential windows of opportunity (gray-shaded regions) for *F. fusca* movement and subsequent spread of TSWV into and among the various plant hosts typically found in local agroecosystems throughout the year. Groves et al. (2001b) demonstrated that perennial and winter annual plant species function as overwintering inoculum sources as well as important sources of TSWV inoculum for spread to susceptible crops, based on their incidence of infection, ability to support reproducing vector populations, and distribution and abundance. Groves et al. (2001a) also demonstrated that both *F. fusca* and *F. occidentalis* began to disperse from senescing overwintering TSWV inoculum sources in early April, with peak flights occurring in mid to late May. Peak intervals of *F. fusca* movement and TSWV incidence in the current study appeared to occur within this window of opportunity for spread from winter annuals to crops and summer annuals at the Higgins location (Fig. 1, location 8) in 1999 (Fig. 5B) and the Sholar (Deep Bottom Road) location (Fig. 1, location 12) in 2000 (Fig. 5C), the two locations with the greatest number of TSWV lesions recorded from *P. hybrida* in each year. The magnitude of immigrating *F. fusca* populations, as well as crop plant susceptibility to TSWV infection (Eckel et al. 1996), are at their peak during this spring interval.

Summer annual weeds may provide a means by which TSWV cycles between overwintering sites in annual plants and back again into winter annual species, or perhaps more permanent hosts such as perennial plants (Fig. 5A). It appears unlikely that summer annuals substantially contribute to TSWV infection in susceptible crops because there is a very limited opportunity to become systemically infected with TSWV and produce populations of potentially viruliferous thrips early in the season (Johnson et al. 1996). However, it will be necessary to more fully characterize vector populations and patterns of TSWV over time in summer annual plant species to more clearly determine their importance in the epidemiology of TSWV. The acquisition of TSWV from infected crops and its inoculation to summer weed hosts appears to be of minor importance in TSWV disease cycles. For this to occur, significant numbers of viruliferous thrips must be produced on TSWV-infected crop plants. Recent studies in pepper, tomato (Gitaitis et al. 1998), and tobacco (McPherson et al. 1992) suggest that very limited numbers of viruliferous thrips are produced on these crops.

Cycling of TSWV from infected summer annual species back into winter annual or perennial species can be inferred from the temporal patterns of *F. fusca* movement and TSWV occurrence that we observed in the fall seasons. For example, patterns of vector and virus movement in the fall season are clearly depicted in Fig. 5B and C, illustrating that movement of *F. fusca* and TSWV occurred over a fairly synchronous and discrete time interval at both locations. As noted earlier, maturation of summer hosts may be less important than hard freezes in inducing fall flights of potential vectors; the first hard freeze of the season effectively forces thrips populations to disperse from these se-

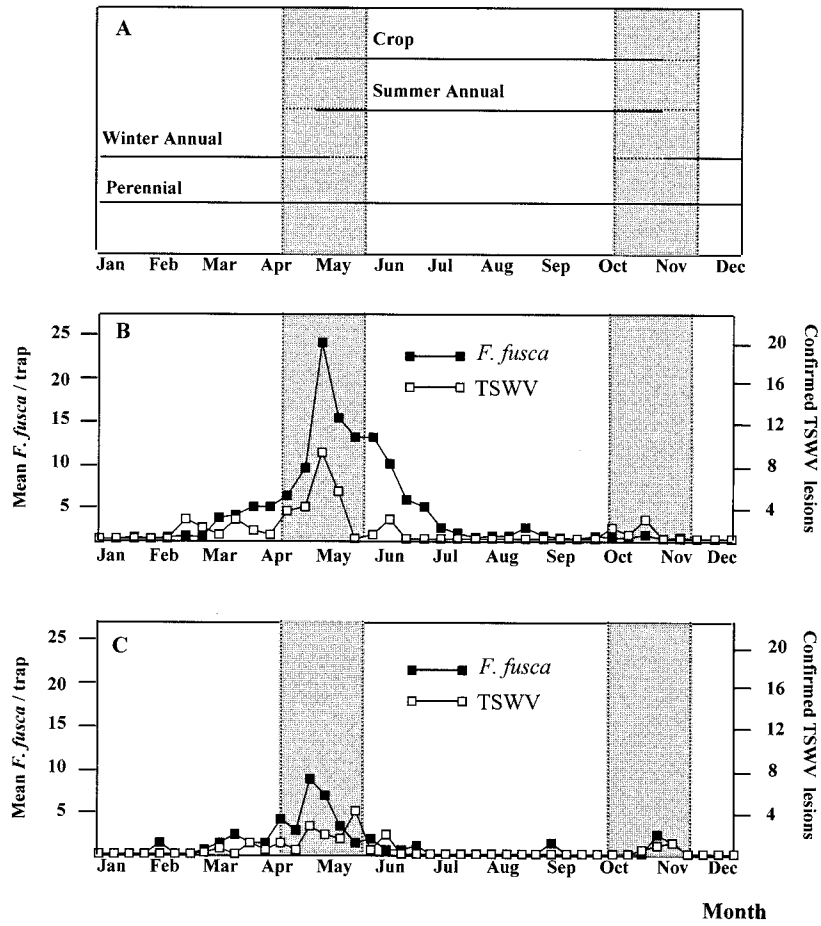

Fig. 5. Conceptual model illustrating the potential windows of opportunity (gray shaded regions) for the spread of TSWV by *F. fusca* among the various plant host types of a local agroecosystem (A). Mean number of TSWV lesions and *F. fusca* collected from Higgins location in 1999 (B) and Sholar (Deep Bottom Rd) in 2000 (C).

nescing summer annual hosts. The observed timing of *F. fusca* movement and TSWV spread in the fall season (Fig. 5A) suggests that summer annual weeds may serve as an over-summering "bridge" for TSWV between overwintering seasons. A better understanding of this relationship between vector flights and virus occurrence is essential to determine when implementation of vector control or weed management practices would be most effective in disrupting the TSWV transmission cycle between winter and summer weeds. Sustainable management of TSWV will most likely require multiple tactics (Cho et al. 1989). Vegetation management to reduce TSWV inoculum requires knowledge of the inoculum source within an area and the physical dimensions of such a source. If inoculum sources are widely distributed among numerous plant species, then TSWV source reduction through vegetation management may not be as successful as a situation where only one or a few plant species in discrete patches serve as inoculum sources.

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