Association of *Frankliniella fusca* and Three Winter Weeds with Tomato Spotted Wilt Virus in Louisiana

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ABSTRACT

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Random surveys of three common winter weed species using the enzyme-linked immunosorbent assay (ELISA) and vector transmission studies demonstrated that tomato spotted wilt tospovirus (TSWV) overwinters in Louisiana. Natural TSWV infection in *Ranunculus sardous*, *Lactuca floridana*, and *Sonchus asper* was detected by ELISA during the winter months and prior to spring vegetable production periods. Recovery of thrips from *R. sardous*, *L. floridana*, and *S. asper* washings yielded all developmental stages of *Frankliniella fusca* during the winter and spring. *Ranunculus sardous* appeared to be the species most often associated with natural TSWV infection and thrips during the winter and prior to spring production periods. *Frankliniella fusca* adults collected from *Ranunculus* spp. from three areas transmitted TSWV to tomato. Other TSWV-vectoring thrips species known to occur in Louisiana were not detected in association with the weed species studied during the winter and spring months. Results of this study suggest that *F. fusca* is an important vector of TSWV in Louisiana.

Since tomato spotted wilt tospovirus (TSWV) was first identified in Louisiana in 1972 (2), it has become a serious problem of several solanaceous crops (3). Although accurate estimates of losses to crop production are unavailable for pepper (*Capsicum* spp.) and tobacco (*Nicotiana tabacum* L.), surveys have shown that incidence of TSWV in commercial tomato fields has averaged 10 to 30% (3). Currently, TSWV is the most important limiting factor in tomato production in Louisiana. Likewise, similar adverse economic impacts caused by the disease have occurred in various crops and ornamentals in most of the southeastern states of the United States (8,19) and worldwide (21).

TSWV is vectored by certain species of thrips including the potato or onion thrips, *Thrips tabaci* Lind. (20), the common blossom or cotton thrips, *Frankliniella schultzei* Tryb. (25), the western flower thrips, *F. occidentalis* Perg. (10), and the tobacco thrips, *F. fusca* Hinds (23). In Japan, the chili thrips, *T. setosus* Moulton (14), has also been shown to transmit the virus. In Taiwan, a tomato spotted wilt-like virus infecting watermelon was shown to be transmitted by *T. palmi* Karney (30).

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Results of a 1985 survey of thrips abundance in Louisiana within tomato (*Lycopersicon esculentum* Mill.) and pepper (*Capsicum annuum* L. and *C. frutescens* L.) fields indicated that *F. fusca, F. occidentalis,* and *T. tabaci* were the only known TSWV vectors present (3). Since *F. occidentalis* was detected in Louisiana for the first time in 1984, it was generally assumed that the expansion of this thrips specie's geographical range was a likely explanation for the increased incidence of TSWV during the early to mid 1980s (11).

Frankliniella fusca and *F. occidentalis* are currently among the most common thrips species present in peanut and solanaceous crops in the southeastern United States (16,17,24,27). *Frankliniella occidentalis* appears to have an affinity for flowers of a wide range of plant species and is more abundant when flowers are present (16,24). Population studies have suggested that seasonal populations of *F. occidentalis* peak during the summer months (16,27). Adults of *F. fusca* continuously reproduce throughout the year in Louisiana and have been found to reach high populations on several species of clover and alfalfa in late winter (18). *Frankliniella fusca* has been reported to overwinter mainly as brachypterous adult females on a variety of winter annuals throughout the southeastern United States (6,9,18). As spring approaches, macropterous adults gradually become more common than brachypterous adults. This is a survival feature that is presumably linked to factors such as temperature, photoperiod, and availability of food (15,18). Stewart et al. (26) reported that adults and larvae of *F. occidentalis* have been found throughout the winter on several crops and weed species in south Texas. However, the overwintering status of this species in the southeastern United States remains uncertain (6).

TSWV is not believed to be seed-transmitted (21); virus inoculum apparently originates from noncultivated areas. Bond et al. (4) reported the presence of TSWV in nine plant genera in Louisiana including spiny amaranthus (*Amaranthus spinosus* L.), blackseed plantain (*Plantago rugelii* Decne.), buttercup (*Ranunculus* spp.), coneflower (*Rudbeckia amplexicaulis* Vahl), horsenettle (*Solanum carolinense* L.), dandelion (*Taraxacum officinale* Wigg.), spiny sowthistle (*Sonchus asper* (L.) Hill), blue vervain (*Verbena brasiliensis* Vellozo), and *Lactuca* spp. Preliminary studies conducted in 1985 in Louisiana suggested that Florida wild lettuce, *Lactuca floridana* (L.) Gaertn., *Ranunculus* spp., and *S. asper* were the most likely overwintering hosts of TSWV (3).

The purpose of this investigation was to identify the overwintering reservoir host(s) and important vector(s) of TSWV responsible for spring infections of solanaceous crops in Louisiana.

MATERIALS AND METHODS

During 1992 and 1993, field studies were performed at four tomato production areas in Louisiana. Plots were located in Calhoun (north central), Lakeland (south central), Chase (northeast), and Wisner (northeast).

Calhoun. The border surrounding a single 21.3 × 80 m plot utilized for vector and host studies extended 50 m beyond the plot border and was allowed to remain undisturbed throughout the winter and spring. During the winter and spring months of 1992, foliage and/or flowers of hairy buttercup, *Ranunculus sardous* Crantz., were collected as a single sample every 2 to 3 weeks to determine the thrips population. In 1993, only flowers of *R. sardous* were collected as four separate samples from four border area quadrants every 2 to 3 weeks for thrips population studies.

Chase. The border surrounding a single 15 × 67 m production plot utilized for weed host and vector studies extended 50 m beyond the plot border and was allowed

to remain undisturbed during the 1992 winter and spring periods.

Lakeland. This site was surrounded by densely wooded areas; therefore, the area designated as border was defined as the 3 to 10 m border between the 30-ha cultivated and wooded areas. This border area was divided into quadrants and left undisturbed prior to and during the growing season.

Wisner. The border surrounding the 1.3 ha production area was unsuitable for reservoir host and vector studies because it was mowed frequently. Therefore, these studies were conducted in an area located within 75 m of the production area. This was divided into four equal quadrants and left undisturbed throughout the study.

TSWV incidence. Incidence of TSWV in *Ranunculus* spp., *L. floridana,* and *S. asper* growing in the vicinity of tomato fields (before planting) was determined periodically during the spring and winter months. In the winter of 1991–92, only the most abundant of these weed species at each site were assayed for TSWV by direct (double antibody sandwich) enzyme-linked immunosorbent assay (ELISA) using a commercially available TSWV-L ELISA kit (Agdia, Inc., Elkhart, Ind.). One hundred to 200 leaf samples of each species were collected at random from the entire area each month. In 1993, estimates of TSWV in the weed species of interest were determined by estimating the percentage of the weed population showing viruslike symptoms within a 50-m border surrounding each field. This was performed by randomly throwing a 1-m-diameter hoop in each of four equally divided quadrants 20 times monthly during March, April, and May and counting individuals of the species of interest. Presence of TSWV in symptomatic plants was confirmed by ELISA.

TSWV transmission by *F. fusca.* In order to determine a possible association between naturally occurring viruliferous thrips and *R. sardous,* immature and/or adult *F. fusca* were collected from these plants at three locations (Lakeland, Calhoun, and Wisner). Thrips were placed in cages with healthy tomato or pepper plants. This weed species was used because it is abundant prior to the spring growing season. The thrips larvae collected were reared to the adult stage by placing them in self-watering acrylic cages (28) and allowing them to feed on virus-free *S. asper* or *R. sardous* leaves grown from seed in a growth chamber. Adult thrips were collected with a fungal spore collector (ERI Machine Shop, Iowa State University, Ames) and placed into 00-size gelatin capsule halves. In 1992, nine to 12 adults were placed at the base of individual 14- to 21-day-old pepper plants (cv. Yolo Wonder) for a test feeding period of 2 days in sealed 7.5-liter white plastic containers. After a 2-day test feeding, the plants were sprayed with abamectin insecticide (Avid 0.15 EC) at a rate of 0.4 ml per liter. Plants were then placed in a growth chamber with a photoperiod of 8 to 10 h at 25°C and observed periodically for symptom development. After 2 to 3 weeks, plants showing viruslike symptoms were tested for the presence of TSWV by ELISA. In 1993, 80 to 290 *F. fusca* adults were placed in five pots containing three young, healthy tomato plants (cv. Pik Red) each in 31.8 × 30.5 × 30.5 cm Plexiglass sleeve cages having openings cut on the top and sides covered with 230-mesh Pe-Cap monofilament polyester screen (Tetko Inc., Elmsford, N.Y.). The cages were placed in a growth chamber with a photoperiod of 12 h and a day/night temperature cycle between 19°C and 25°C. After a feeding period of approximately 1 week, the plants were taken from the cages and sprayed with abamectin and acephate (Orthene 15.6 EC) at a rate of 0.4 ml per liter and 22.2 ml per liter, respectively. Plants were then placed in a greenhouse and observed for 2 to 3 weeks. Symptomatic plants were tested for TSWV by ELISA. To insure that the greenhouse was free of thrips, an insecticide spray program was followed.

Weed abundance. To assess the role of *S. asper, L. floridana,* and *Ranunculus* spp. as sources of TSWV, their abundance in the crop vicinity was determined monthly during the spring at three locations (Calhoun, Wisner, and Lakeland). The border around the production areas of each site was divided into four quadrants. Weed abundance was estimated by randomly throwing a 1-m-diameter hoop 20 times into each quadrant and recording weed species frequency. The most common maturity stage of these weed species was also recorded.

Foliage washings. To identify and quantify the number of thrips associated with winter annuals, foliage samples were collected periodically from all locations. Thrips colonizing the weed species of interest were recovered from a 500-g composite sample of whole plants. Samples were agitated vigorously with a 5% deter-

Table 1. Natural incidence of tomato spotted wilt virus (TSWV) in weed species collected from border areas near solanaceous crop production plots in Lakeland, Calhoun, and Chase, La., during the winter and spring of 1992

		Weed species[a]		
Location	**Month**	***Lactuca floridana***	***Sonchus asper***	***Ranunculus sardous***
Calhoun	January	48 (0)[b]	188 (0)	282 (4)
	February	...[c]	130 (0)	200 (3)
	March	...	117 (0)	185 (9)
	April	...	...	213 (12)
	May	...	...	236 (16)
Lakeland	January	...	58 (5)	...
	February	...	184 (0)	...
	March	60 (1)	134 (0)	...
	April	108 (0)	...	69 (0)
	May	542 (3)	...	...
Chase	February	...	200 (0)	...
	March	...	200 (0)	...
	April	...	194 (1)	...

[a] Individual plants were selected randomly throughout the sites.
[b] Number of individuals tested followed by the number of positive reactions in parentheses. Presence of TSWV was determined by enzyme-linked immunosorbent assay. Positive samples were confirmed by mechanical transmission on pepper cv. Yolo Wonder.
[c] Samples not collected.

Table 2. Natural occurrence of *Ranunculus sardous*, *Lactuca floridana*, and *Sonchus asper* in border areas near solanaceous crop production plots of Lakeland, Calhoun, and Chase, La., during the spring months of 1993

		Weed species[a]		
Location	**Month**	***L. floridana***	***S. asper***	***R. sardous***
Lakeland	March	4.3 (V)[b]	6.7 (R)	<0.1 (V)
	April	0.7 (V)	1.8 (R)	0.0
	May	1.5 (V)	0.4 (R)	0.0
Wisner	March	0.0	0.0	23.1 (V)
	April	0.0	<0.1 (V)	15.3 (R)
	May	0.0	0.0	19.4 (R)
Calhoun	March	<0.1 (V)	0.3 (R)	17.2 (V)
	April	0.0	<0.1 (V)	12.8 (R)
	May	0.0	0.0	9.8 (R)

[a] Average number of plants counted within the circumference of a 1-m-diameter hoop thrown randomly 20 times in each of four quadrants (80 total) at each site. The assessments were done at all sites between the 10th and 20th of each month.
[b] Most common maturity stage present: V = vegetative; R = reproductive (flowering) stage.

gent solution in a plastic bag. All thrips filtered from the wash solution were counted using a dissecting microscope at 24× and mounted in an insect mounting solution on microscope slides for identification.

RESULTS

Overwintering hosts of TSWV. In random surveys throughout the state, during the winter months TSWV infection was detected in *L. floridana, S. asper,* and *R. sardous*. TSWV incidence at Lakeland was very low for all three weed species throughout the study with the exception of an unusually high incidence of virus in *S. asper* in January of 1992 (Table 1). TSWV was detected at Calhoun in 1992 in *R. sardous* with a gradual increase in incidence from January to early summer (Table 1). *Lactuca floridana* and *S. asper* were present in low numbers at this site, and TSWV was not detected in those species. Populations of the weed species of interest at Chase were very sparse in 1992, and only one individual of *S. asper* tested positive for TSWV (Table 1).

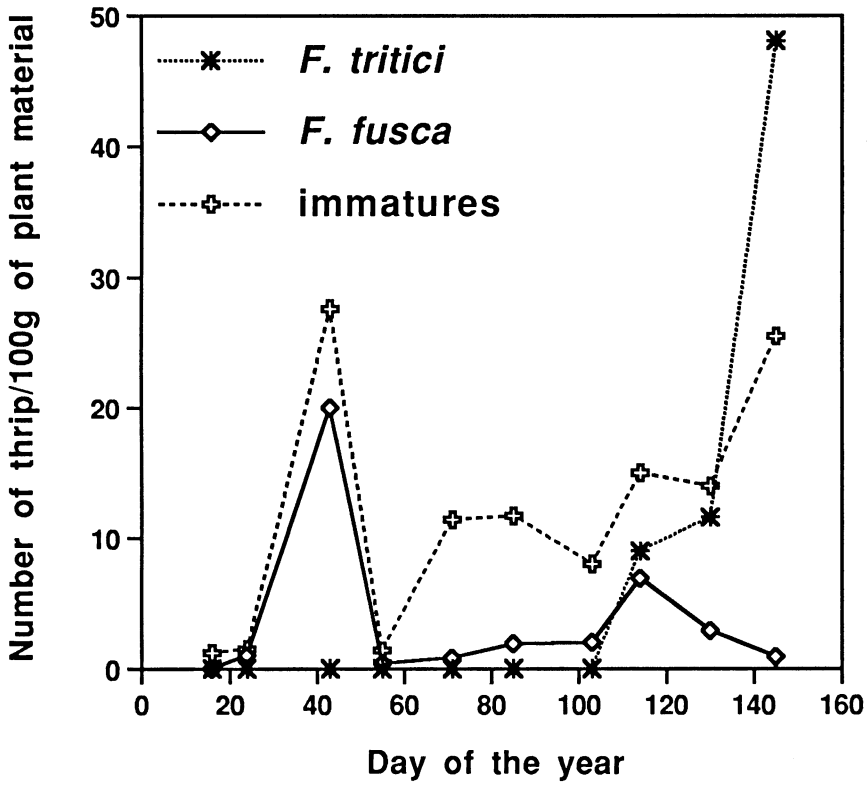

Fig. 1. Seasonal abundance of thrips associated with whole plants of *Ranunculus sardous* at Calhoun, La., during the winter and spring of 1992.

Table 3. Occurrence of TSWV-vectoring *Frankliniella fusca* adults collected from *Ranunculus sardous* flowers located near three solanaceous crop production plots of Louisiana in the spring of 1993

Location	Collection date[a]	Quadrant	Number of thrips	Transmission[b]
Lakeland	March 24	I	180	+
	March 24	II	80	–
	March 29	III	110	–
	March 29	IV	200	–
	April 14	I	290	–
	April 14	II	90	–
	April 12	III	160	–
	April 12	IV	100	–
	April 26	II	100	+
	April 26	III	175	–
Calhoun	May 4	I	125	–
	May 4	II	200	–
	May 4	III	200	–
	May 4	IV	200	+
Wisner	May 14	I	200	–
	May 14	II	200	+
	May 14	III	180	+
	May 14	IV	230	–

[a] Adult thrips were randomly collected with a fungal spore collector and identified with a dissecting microscope.

[b] Thrips collected on each date were placed in cages containing 15 3-week-old tomato plants. Three weeks later, symptomatic plants were tested by enzyme-linked immunosorbent assay. Asymptomatic plants were not tested.

In 1993, a weed community assessment was performed at each location to determine species abundance, seasonal maturation stage, and abundance of individuals with viruslike symptoms. Results of this experiment are shown in Table 2. *Ranunculus sardous* was very common at Wisner and Calhoun; however, it was sparse at Lakeland. *Sonchus asper* and *L. floridana* were variable at all sites. *Sonchus asper* populations declined by April; however, *R. sardous* populations were still blooming in May. *Lactuca floridana* populations remained relatively unchanged throughout the spring.

In 1993, only *R. sardous, S. asper,* and *L. floridana* plants with virus symptoms were tested for TSWV by ELISA. Less than one percent of the weeds were symptomatic, and only 12 *R. sardous* samples obtained from Wisner and Calhoun on May 15 tested positive for TSWV (data not shown).

Association of TSWV-vectoring thrips with overwintering hosts. *Frankliniella fusca* was found to be active on *R. sardous* during the winter months at Calhoun in 1992 and 1993. In 1992, whole plant washings demonstrated that adults of *F. fusca* were present on this weed in different levels from January to May (Fig. 1). Adults of *F. tritici,* a nonvector (21), were recovered in the months of April and May.

Immature thrips were recovered from *R. sardous* during this study. Individuals were placed in Tashiro cages and reared to the adult stage on leaves of *R. sardous* and *S. asper* in the laboratory. Seventy-nine immatures collected from *R. sardous* rosettes from 16 January to 10 March were determined to be *F. fusca.* A single collection of immature thrips from *R. sardous* flowers on May 8 was found to contain both *F. fusca* and *F. tritici.*

Similar thrips population assessments were conducted at Lakeland and Chase in the winter of 1992 with *S. asper* and *L. floridana. Frankliniella fusca* adults were recovered in low numbers from *S. asper* and *L. floridana* at these two locations.

Immatures of *F. fusca* were recovered from both winter weeds at Lakeland, which suggests that at least some reproduction was occurring on these two weed species.

Transmission of TSWV by field-collected *F. fusca*. Transmission tests to pepper in 1992 using 875 field-collected immatures and adults of *F. fusca* (9 to 12 per plant) from a variety of sites in Louisiana failed to provide evidence of naturally occurring viruliferous thrips.

In 1993, tomato plants used in transmission test feeding periods with thrips collected on 24 March and 26 April from Lakeland were positive for TSWV by ELISA (Table 3). This demonstrates that at least one viruliferous thrips was present in each test group that tested positive. Viruliferous thrips were not detected in other transmission tests conducted with 1,205 additional *F. fusca* individuals collected at Lakeland. Viruliferous thrips were also detected at Calhoun and Wisner (Table 3).

DISCUSSION

The epidemiology of TSWV is poorly understood, particularly the overwintering period. The virus must be associated with a host or vector in order to survive the winter. Plant hosts of TSWV can be found in Louisiana throughout the year; however, their number is reduced during the winter. Of the possible hosts, only *L. floridana, S. asper,* and *Ranunculus* spp. were shown to be infected with TSWV in the field during the winter. *Lactuca floridana* is considered to be biennial in Louisiana. This plant emerges in October and senesces in late summer. *Ranunculus sardous* and *S. asper* are both winter annuals. They emerge in fall or winter and senesce in the spring. Some *S. asper* plants mature sporadically throughout the year.

Consistency in the selection of weeds for TSWV assays was not possible mainly because of variation in seasonal maturation and low infection levels. Therefore, general trends of seasonal infection of weed hosts of TSWV could not be elucidated throughout the state. It is possible that TSWV incidence in weed populations of a particular species may be affected by distribution of that species in relation to other plant species. The occurrence of plants of one species as small isolated populations could result in variation in incidence due to limited thrips vector movement from one population to another. This may explain the erratic levels of incidence of TSWV found in *S. asper* in Lakeland in 1992 (Table 1). In contrast, large areas of one weed host may allow a steady increase in the incidence of TSWV-infected plants due to easy movement of thrips from plant to plant. This may be the reason for the apparent continual increase of TSWV incidence in *R. sardous* at Calhoun from winter through the spring.

The results of TSWV detection using only symptomatic plants in the 1993 weed community assessment studies were difficult to interpret. Moreover, infections were difficult to detect on a visual basis. These winter annuals in some cases were very small in size and grew slowly in cold weather thus making virus symptoms difficult to see. This is not surprising, since Hsu and Lawson (13) showed the existence of asymptomatic tospovirus-infected *Impatiens* spp. after inoculated plants were subjected to a period of relatively cool temperatures.

Presence of the virus in winter annuals demonstrates that the virus overwinters in Louisiana. Prior to this study, presence of TSWV in natural weed hosts in the continental United States during the winter months was not documented. TSWV replicates in the thrips vector (29) and there have been some suggestions that the virus may overwinter in thrips pupae in the soil (6). It is possible that these mechanisms also could be involved in the epidemiology of the virus in Louisiana.

Only one of the three known thrips vectors of TSWV was found in this study as adults in Louisiana during the winter months. *Thrips tabaci* can be found around the petioles of onions in late winter, but this species was not associated with the TSWV-susceptible hosts studied. *Frankliniella occidentalis* was not associated with the winter weeds of interest, but it has been reported to occur on a variety of plants throughout the winter in the southeastern United States (6,7). *Frankliniella fusca* adults were present on all three winter weeds of interest during this period, suggesting that this species is capable of surviving temperatures below freezing. In South Carolina, it has been reported that this thrips species is capable of surviving periods of freezing temperatures as adults on plants such as crabgrass, broomsedge, and bermudagrass at or near the soil line (9). Since *R. sardous* is mainly prostrate during the winter, the microenvironment near the soil may protect thrips from cold temperatures.

TSWV can only be acquired for transmission by immature thrips (1,21); therefore, it was important to identify the species of thrips that were actively reproducing on these weeds. *Frankliniella fusca* was the only thrips species found on the weed populations that harbored the virus during the winter and, more significantly, prior to crop infection in the spring. The fact that leaves of *S. asper* were occasionally used in the propagation of immature thrips derived from *R. sardous* may have influenced interpretations of the results. Propagation of thrips in the laboratory can be difficult, and the mortality rate can be high. Although the results were consistent with the adult populations recovered from the winter annuals, it is possible that other thrips species may have been more sensitive to the rearing conditions, and their larvae may have died before reaching the adult stage.

Frankliniella fusca was utilized in TSWV-transmission experiments with field-collected thrips since this species was found on *R. sardous, S. asper,* and *L. floridana.* Moreover, *F. fusca* was relatively easy to identify with a dissecting microscope. The detection of viruliferous thrips at all three sites in the spring of 1993 provided strong evidence for the involvement of *F. fusca* in the epidemiology of the virus in susceptible spring crops. Moreover, the majority (approximately 80%) of all the adults collected were macropterous and thus capable of flying. Brachypterous thrips of the same species are capable of TSWV transmission but cannot fly and therefore can transmit the virus only on a local basis. In Georgia (5), ELISA detection of TSWV in *F. occidentalis* and *F. fusca* adults collected from volunteer and transplanted peanut and evening primrose (*Oenothera laciniata* Hill) in the winter and spring of 1990–91 further suggests the involvement of these thrips species as vectors of TSWV. However, in this case, the evidence is not conclusive since detection of TSWV within adults does not necessarily mean that the virus was acquired at the larval stage and thus capable of being transmitted.

Frankliniella fusca, T. tabaci, and F. occidentalis have been shown to transmit TSWV at a relatively equal rate of efficiency (22,23). Of all the thrips species found in tomato fields in Louisiana, *F. fusca* is likely to be the most important vector of TSWV. Adults of this species are frequently associated with, and actively reproducing on, TSWV-infected winter weeds prior to crop infection. This species has been shown to be capable of acquiring the virus from *L. floridana, S. asper,* and *R. sardous* and transmitting it to *S. asper* and *C. annuum* in the laboratory (12).

The movement of viruliferous thrips, both by natural and artificial means, has most likely contributed to the rapid spread of the virus worldwide (8). Moreover, the apparent inability of insecticides to prevent virus transmission has stalled efforts for developing chemical control practices for the disease (8). The results of this study along with previous studies (8) suggest that general maintenance practices that reduce the number of virus hosts present around production areas could reduce infection by TSWV. However, attempted control of populations of thrips and weeds should precede spring production periods.

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