Temporal Relationship of Thrips Populations to Tomato Spotted Wilt Incidence in Tomato in the Field[1]

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Abstract Thrips-transmitted *Tomato spotted wilt* (TSW) *virus* (Family Bunyaviridae Genus *Tospovirus*) is an important problem in tomato in the southeastern United States. Tobacco thrips, *Frankliniella fusca* (Hinds), and western flower thrips, *Frankliniella occidentalis* (Pergande), (Thysanoptera: Thripidae) are the known major vectors of TSW virus in Georgia; however, the temporal relationship of thrips to TSW disease incidence in tomato is not clear. Field studies were conducted in 2005 and 2006 specifically to compare thrips population dynamics to disease incidence in untreated tomato fields. Populations of *F. fusca* were observed to increase approximately 3 wks prior to increased TSW incidence and correlated positively with TSW when considering this delay. Populations of *F. occidentalis* positively correlated with TSW occurrence in 2005, but not in 2006. Additionally, tomato fruit yield decreased greater in plants with early TSW symptoms than in plants that developed symptoms later in the season. Both results suggest early-season thrips management targeted at *F. fusca* during the early-growth stages of tomato could help to reduce the risk of yield loss in tomato due to this disease.

Key Words tomato spotted wilt virus, *Frankliniella fusca*, *Frankliniella occidentalis*, *Solanum lycopersicum*

Thrips-transmitted *Tomato spotted wilt virus* (TSWV, Family Bunyaviridae; Genus *Tospovirus*) which causes the disease, tomato spotted wilt (TSW), has had devastating consequences on crop production world-wide (Goldbach and Peters 1994, Persley et al. 2006). Average annual losses in Georgia from 1996 - 2006 due to TSW were estimated to be $12.3 million in peanut, $11.3 million in tobacco and $9 million in tomato and pepper (Riley et al. 2011). In tomato, *Solanum lycopersicum* L., the infected foliage develops reddish-brown ring spots, and the interveinal speckling coalesces into necrotic lesions (Best 1968, Gitaitis 2009). TSW during early-growth stages of tomato plant can lead to severe stunting or wilt stress with the earlier symptoms resulting in greater yield loss (Chaisuekul et al. 2003, Moriones et al. 1998). The fruit disease symptoms appear as yellow ring spot or necrotic spots (Best 1968). In fresh market tomato, mature green fruit may be harvested as marketable fruit and then the TSW irregular ripening may appear after the fruit ripen following treatment with ethylene

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(Olson 2009). Management of thrips and TSW in tomato has been shown to be cost effective (Fonsah et al. 2010).

Among the various thrips species (Thysanoptera: Thripidae) that transmit TSW virus in the USA (Riley et al. 2011), tobacco thrips, *Frankliniella fusca* (Hinds), and western flower thrips, *Frankliniella occidentalis* (Pergande), are the main vectors of TSW virus in Georgia (Riley and Pappu 2000, 2004). In spring, thrips larvae acquire the virus after feeding on infected weeds around the vegetable field prior to tomato planting and migrate to the crop when transplanted (Groves et al. 2001, 2002). Within 1 - 2 wks, as these immatures develop into adults and the acquired virus replicates in the thrips, the virus is readily transmitted to healthy tomato plants through adult thrips feeding (Ullman et al. 1997). Noninfectious adults that feed on infected plants are unable to subsequently transmit the virus (Wijkamp et al. 1996). The virus is not passed from adults to offspring via the egg and only 1st and 2nd instars can acquire the virus; thus, each generation of thrips must reacquire the virus from a host plant that supports thrips reproduction (Peters et al. 1996, Ullman et al. 1997, Wijkamp et al. 1995).

Temporal patterns of *F. fusca* dispersal and TSWV incidence generally show an increase to a peak between April and June as reported in North Carolina (Groves et al. 2003), eastern Virginia (Nault et al. 2003), and South Georgia (Riley and Pappu 2004). Moreover, an increased occurrence of *F. fusca* on yellow sticky traps was positively correlated to TSW incidence in the TSW virus indicator plant, *Petunia hybrida* hort. ex Elisa de Vilmorin (Groves et al. 2003), and beat cup samples (Riley and Pappu 2004). Spring dispersal of thrips is most likely influenced by temperature and other factors such as precipitation (Groves et al. 2003, Kirk 1997, Lewis 1997, Morsello and Kennedy 2009, 2010, Olatinwo et al. 2010). Increasing temperatures in spring may result in increased development rates and population growth; whereas, rainfall negatively affects thrips populations by larval mortality and suppressing adult flight (Kirk 1997, Lewis 1997). In the southeastern USA, the population dynamics and role of *F. occidentalis* in the TSW virus epidemiology in tomato has been less well understood (Stumpf and Kennedy 2007). The reproductive rate of *F. occidentalis* populations is strongly influenced by the host quality, especially the presence of pollen for food (Kirk 1984, 1985, Riley et al. 2007, 2010). However, the temporal dynamics of these two thrips species in relation to the incidence of TSW in tomato in the field need further investigation. The main objectives of this study were to: (1) correlate temporal TSW incidence in untreated tomato fields with the seasonal fluctuation of the vectors, *F. fusca* and *F. occidentalis,* and (2) determine the relationship between incidence of TSW and susceptible tomato fruit yield under field conditions in Georgia.

Materials and Methods

The field studies were conducted each spring in 2005 and 2006 at the Coastal Plain Experiment Station, Tifton, GA, on TSW-susceptible tomato cultivars not treated with insecticides effective against thrips. Soil type was a Tift pebbly clay loam soil or sandy loam. All field tests used methyl-bromide fumigated beds at the rate of 224 kg/ha (98:2, Hendrix and Dail, Tifton, GA). Fertilizer rates for tomato were 925 kg/ha of 6 - 6-18 (Fletcher Limestone Inc., Tifton, GA) and tomatoes were maintained with standard plastic-cultural practices for staked tomatoes and were spaced 46 - 61 cm on a 1.8 m wide bed with 1.5 m wooden stakes between plants.

In 2005, 'FL 47' (TSW-susceptible tomato hybrid, Victory Seed Company, Molalla, OR) seedlings were transplanted with 61-cm row spacing into 1 row (1.8 m wide) black plastic mulched beds in 17 m long plots on 11 April 2005. There were 16 rows with 50 plants per row. In 2006, 'Marglobe' (TSW-susceptible tomato variety, USDA) was planted on 23 March with same spacing as in 2005, but each row was 30.5 m long and there were 10 rows with 70 plants per row. In both years, the tomato field was only treated with a fungicide (Ridomil Gold-Bravo® WP 2.2 kg product/ha, Syngenta, Greensboro, NC) for fungal disease and a *Bacillus thuriengensis* Berliner (DiPel® 2.2 kg product/ha, Valent U.S.A. Corporation, Walnut Creek, CA) for armyworm control. These pesticides allowed for a natural increase in thrips populations.

Tomato plants were monitored for TSW symptoms on foliage and fruits (Gitaitis 2009). Disease ratings were made on: 21 and 28 April; 6, 13, 19, and 26 May, and 3 and 9 June in 2005; 7, 11, 19, and 25 April; 2, 9, 15, and 22 May in 2006. The number of plants with foliar TSW symptoms per row was recorded weekly throughout the season, and percent TSW incidence was calculated. A single, fully-expanded terminal leaflet was randomly collected from the top third of each of 10 plants after fruit set in 2005 from each plot to detect TSWV with enzyme-linked immunosorbant assay (ELISA) using a TSWV detection kit. A sample was deemed positive for TSWV if the absorbance reading was 3X the value of a known uninfected sample.

For both years, beat-cup and yellow sticky trap samples were used to determine the total number of thrips by species. Beat cup samples were collected on: 21 April, 6, 17, 27, May, and 1 and 9 June in 2005; 4, 11, 18 and 25 April; 2, 9, 15 and 23 May in 2006, whereas yellow sticky trap samples were removed from field on: 18 and 25 April, 2, 10, 17 and 24 May, and 2 June in 2005; and 5, 12, 19 and 26 April, and 3, 10, 17 and 24 May in 2006. Beat cup samples were taken per 10 subplots per row per week; the details of this procedure are described in Joost and Riley (2004). Yellow sticky traps (7.62 × 12.7 cm yellow, Olson Products, Medina, OH) were set up in the center of the plot and were exposed for a week per row. The identification keys developed by Oetting et al. (1993) and Stannard (1968) were used to identify the adult thrips sampled under 70 - 140X magnification of SZH10 Olympus® (Olympus America, Lake Success, NY) stereomicroscope.

Individual plants that expressed TSW symptoms were color tagged on weekly basis. These plants were at different growth stages when the disease symptoms were expressed. Plants started showing TSW symptoms as early as 3 wks after planting which was consistent with the observations of Moriones et al. (1998) and Accotto et al. (2005). Tomato fruits were harvested individually when matured and were separately bagged from each color-tagged plant on 14 and 23 June in 2005; and 19, 25 April, and 2, 9, 15, and 22 May in 2006. At the time of harvest, fruits were evaluated and were classified into marketable categories by size according to the USDA standards set for fresh market tomato (Sargent and Moretti 2004). However, damaged fruits consisted of a single damage category, TSW symptomatic fruit and thrips damaged fruit (Olson 2009). Unmarketable fruit from caterpillar-damaged fruits (Lepidoptera: Noctuidae) and physiologically damaged fruits (blossom end rot), which was a minor component in both years, were excluded in yield evaluations.

Analysis of variance was conducted using PROC GLM (SAS Institute 2003), and separation of means for TSW incidence or thrips species was done on weekly basis as determined by LSD tests. Sampling week and plant rows were considered as temporal and spatial independent variables, respectively. For the analysis to determine the effect of TSW on fruit yield, individual tomato plants with same color-tag were considered the replicates. Correlations between thrips in beat cup or yellow sticky trap and TSW occurrence on the weekly basis were conducted using PROC CORR procedure of SAS. However, because TSW symptom development in transplant-age tomato plants requires 2 - 5 wks from thrips inoculations (Chaisuekul et al. 2003), the thrips numbers were delayed by up to 5 wks relative to symptom incidence to find the best average correlation.

Results and Discussion

Based on a weekly survey for TSW symptoms, the seasonal average (± SE) percent TSW incidence on tomato plants was 28.6 ± 2.8 in 2005 and 38.0 ± 4.3 in 2006. The final incidence at the time of harvest was 81 ± 3% for 2005 and 92 ± 2% for 2006, so the disease pressure was severe in both years (Fig. 1a, 2a). In 2005, the ELISA-confirmed TSW infected was 63 ± 24%. Seasonal estimates of thrips populations as determined by beat cups for the spring crop of 2005 and 2006 included *F. fusca* (2.0 ± 0.2 and 4.2 ± 0.6, respectively), *F. occidentalis* (18 ± 2.8 and 0.10 ± 0.04 and 5.2 ± 0.9, respectively), and the non vector species *F. tritici* (2.0 ± 0.3 and 5.2 ± 0.9, respectively). In addition, *F. fusca* collected in yellow sticky traps were 52 ± 5 and 93 ± 18 in 2005 and 2006, respectively. These data suggest that the TSW incidence was fairly consistent in both years, but abundance of thrips species that vector the TSW virus, *F. fusca* and *F. occidentalis*, differed markedly between years.

In 2005, the first TSW symptomatic plant was noticed 1 wk after planting and, subsequently, TSW occurrence significantly progressed (F = 264; df = 7, 104; P < 0.001) reaching peak level by Week 8 (Fig. 1a). *Frankliniella fusca* captured on the yellow sticky traps sharply increased (F = 64.3; df = 6, 90; P < 0.001) in density between Week 3 and 5 (Fig. 1b), but the increase was on a relatively smaller scale in the beat cup samples (F = 17.9; df = 5, 75; P < 0.001; Fig. 1c). Although *F. occidentalis* density collected in beat cup sample was initially low, their density spiked (F = 92.5; df = 5, 75; P < 0.001) by Week 6 with a steady decline in the following 2 wks (Fig. 1d). Overall density of *F. tritici* collected for the 2005 season was relatively low in 2005 season, but a significant increase (F = 41.6; df = 5, 75; P < 0.001) was seen by Week 6 (Fig. 1d).

In 2006, the first tomato plant detected with a TSW symptom was delayed by 3 wks. The density of TSW plants gradually increased until Week 6, then sharply increased (F = 345; df = 7, 63; P < 0.001) between Week 6 and 7 (Fig. 2a). Dispersal of *F. fusca* collected in yellow sticky traps were noticeably high in the Week 4 (F = 61.7; df = 7, 62; P < 0.001) followed by a sharp decline in the following week (Fig. 2b). A similar, but delayed progression in *F. fusca* density was observed in beat cup samples with the greatest density was in Week 5 (F = 11.3; df = 7, 63; P < 0.001; Fig. 2c). Relative to the previous year (2005), *F. occidentalis* was less dense in 2006, but a slight peak (F = 2.9; df = 7, 63; P < 0.01) was noticed in Week 4 (Fig. 2d). Populations of *F. tritici* increased by Week 6 (F = 11.9; df = 7, 63; P < 0.001) and remained at same level during Week 7 then sharply declined.

When comparing samples on the same date as collected, a negative correlation between TSW incidence and *F. fusca* density, and a positive correlation between TSW and *F. occidentalis* was observed in 2005 (Table 1). However, studies have shown that TSW symptoms generally appear in field tomato plants weeks after transmission (Accotto et al. 2005, Chaisuekul et al. 2003, Moriones et al. 1998). Therefore, the relationship between thrips counts and disease occurrence was assessed by delaying the thrips incidence by 1, 2, 3, 4 and 5 weeks and then correlating with TSW

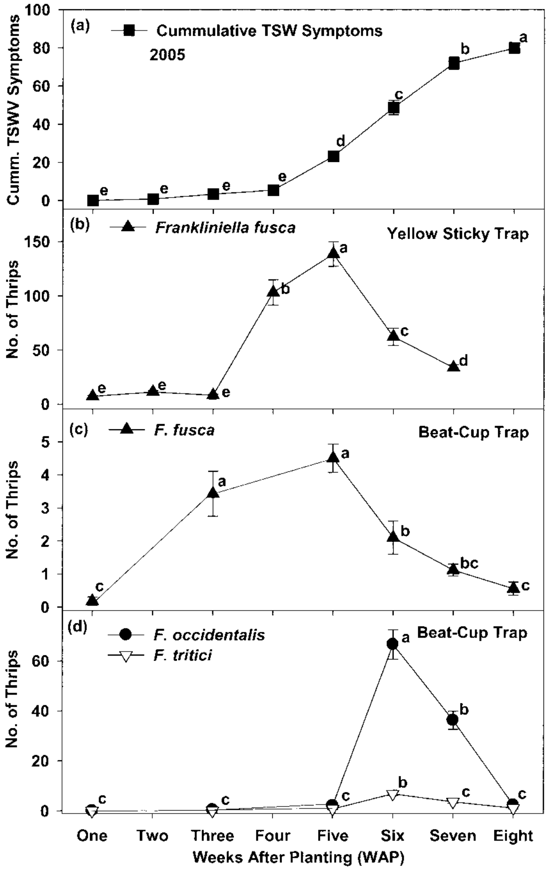

Fig. 1. Mean (± SE) (a) cumulative percentage of TSWV foliar symptoms expressed in tomato plants per row (n = 50 plants), (b) total *F. fusca* sampled after weekly exposure of yellow sticky trap per row, (c) total *F. fusca*, and (d) total *F. occidentalis* collected per 10 subplots per row using beat cups through weeks after planting (planting on 11 April 2005) of TSWV-susceptible tomato cultivar "FL 47" in spring 2005. Means followed by the same letter among the sample weeks are not significantly different (LSD Test, $P < 0.05$).

incidence. When we did this, the best correlation was observed when *F. fusca* counts were delayed by 3 weeks in both yellow sticky traps and beat cup samples in 2005 (Table 1). The best positive correlation between TSW and *F. occidentalis* in beat cup samples was noted when seasonal occurrence of *F. occidentalis* was delayed by 1 week (Table 1). Spatial correlations by individual rows suggest that F. fusca was positively related to TSW (r = 0.51; n = 16; $P < 0.05$) by Week 2 in yellow sticky traps during 2005. Similarly, F. occidentalis was spatially correlated with TSW by Week 3 in 2005 (r = 0.53; n = 16; $P < 0.05$), Week 5 in 2006 (r = 0.79; n = 16; $P < 0.01$).

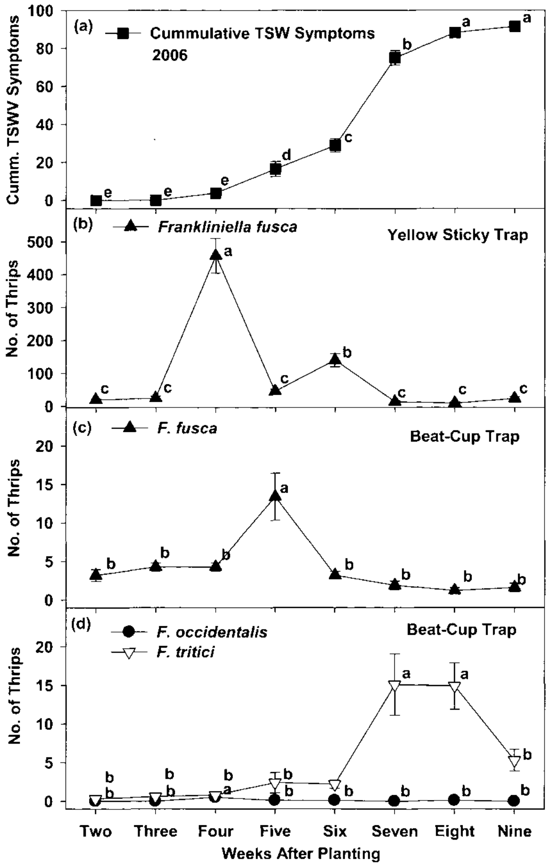

Fig. 2. Mean (± SE) (a) cumulative percentage of TSWV foliar symptoms expressed in tomato plants per row (n = 70 plants), (b) total *F. fusca* sampled after weekly exposure of yellow sticky trap per row, and (c) total *F. fusca*, and (d) total *F. occidentalis* collected per 10 subplots per row using beat cups through weeks after planting (planting on 23 March 2006) of TSWV-susceptible tomato cultivar "Marglobe" in spring 2006. Means followed by the same letter among the sample weeks are not significantly different (LSD Test, P < 0.05).

In 2006, significant positive association between *F. fusca* and TSWV incidence was noted when the thrips density was delayed by 3, 4, 5 weeks in both yellow sticky traps and beat cups (Table 1). There was a stronger positive correlation between TSW incidence and *F. fusca* density in yellow sticky trap (r = 0.85; n = 20; P < 0.001) when the increase in *F. fusca* density during third and fourth WAP were correlated with the increased TSWV incidence disease in Week 6 and 7. Similarly, beat cup samples of *F. fusca* during Week 4 and 5 correlated more positively (r = 0.71; n = 20; P < 0.001) with increased occurrence of TSW plants during the Week 6 and 7. However, no

Table 1. Pearson's correlation between thrips sampled and TSW incidence in tomato by plot.

			TSW incidence relative to thrips counts (No.) weeks earlier					
Year	Method	Thrips spp.	(0)	(1)	(2)	(3)	(4)	(5)
2005	BC	*F. fusca*	–0.28** (96)	-	0.32** (64)	0.68*** (48)	0.66*** (32)	0.64*** (32)
	YST		-	0.34*** (112)	0.69*** (96)	0.77*** (80)	0.56*** (64)	-
2006	BC		–0.33** (80)	–0.23* (70)	-	0.30* (50)	0.42** (40)	0.52** (30)
	YST		–0.36 (80)	-	-	0.39** (50)	0.39* (40)	0.43* (30)
2005	BC	*F. occidentalis*	0.36*** (96)	0.69*** (80)	0.60*** (64)	0.63*** (48)	0.39* (32)	0.37* (32)
2006	BC		-	-	-	-	-	-

The notations indicate the significant correlation (*P*: * < 0.05; ** < 0.01 and *** < 0.001) between thrips and TSWV incidence. The abbreviations are: BC = beat cup and YST = yellow sticky trap. The parentheses indicate the number of rows per week (N).

correlation was detected between TSW and *F. occidentalis* with or without delay (Table 1).

Data suggested that time of TSW incidence relative to plant age significantly affected marketable fruit yield (Figs. 3a, b). In 2005, marketable fruit yield per plant by weight ($F = 8.5$; df = 7, 66; $P < 0.001$) and number ($F = 14.0$; df = 7, 66; $P < 0.001$) was significantly low until Week 8 at which TSW incidence did not impact marketable fruit yield per plant. In addition, percent TSWV-damaged fruits per plant were significantly greater (> 80%) up to Week 7 ($F = 5.1$; df = 7, 66; $P = 0.001$); thereafter, the loss due to TSW damage on fruit reduced. In 2006, marketable fruit yield per plant showed the same pattern as in 2005, where fruit weight ($F = 3.7$; df = 5, 111; $P < 0.01$) and number ($F = 9.3$; df = 5, 111; $P < 0.001$) were significantly higher when TSW incidence

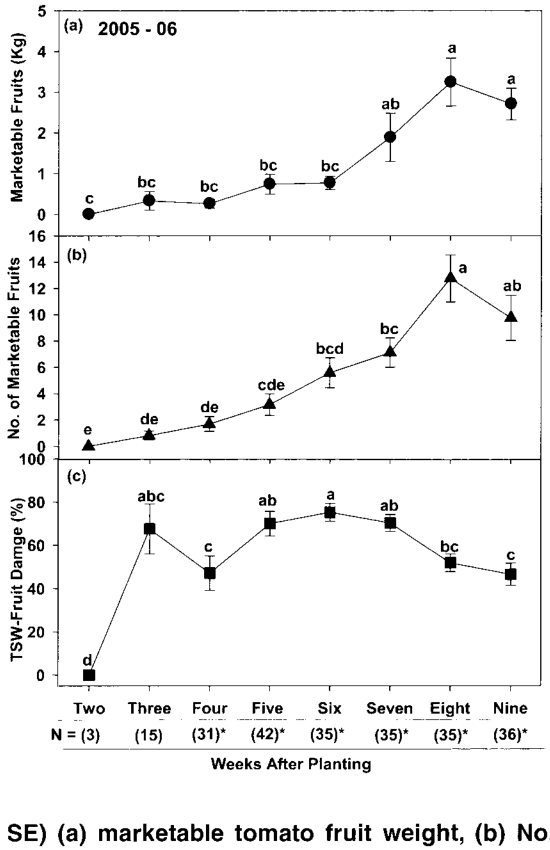

Fig. 3. Mean (± SE) (a) marketable tomato fruit weight, (b) No. of marketable fruits, and (c) percent TSWV-damaged fruits per plant that first expressed TSWV symptoms weeks after planning in spring 2005 and 2006 combined. Tomato was planted on 11 April 2005 and 23 March 2006. The parentheses indicate the number of plants per week (N) expressed TSWV symptoms. * indicate the weeks that include both years' data. Means followed by the same letter among the sample weeks are not significantly different (LSD Test, $P < 0.05$).

appeared late during Week 8 and 9. However, there was no significant difference (F = 1.6; df = 5, 97; P = 0.17) in the percentage of TSWV-damaged fruit regardless of the time of TSW symptom occurrence in 2006. When both the years were combined, the percentage of TSWV-damaged fruits across weeks remained relatively constant (Fig. 3c). In summary, the earlier the TSW symptom appearance, the lower the tomato yield, similar to the observations by Moriones et al. (1998).

During both years, *F. fusca* counts best correlated with TSW symptom development approx. 3 weeks later. Based on previous studies, TSW symptoms appear on tomato plants 2 or 3 wks after exposure to viruliferous-thrips in tomato field (Accotto et al. 2005, Moriones et al. 1998). Chaisuekul et al. (2003) demonstrated that this delay between thrips inoculation and symptom development could be as much as 5 wks for a 4-wk-old tomato plant (i.e., transplant age). The consistent delay between *F. fusca* and TSW symptom development and positive correlation in both years based on this delay suggest that this vector species was a more consistent vector of TSW virus in tomato than *F. occidentalis* at this location.

Our results also showed that tomato fruit yield is more severely impacted if the TSW symptom occurs during the early stages of the crop. This was consistent with previous studies on TSW in tomato (Moriones et al. 1998). It follows that an effective management of TSW in tomato requires preventative tactics (Riley and Pappu 2000, 2004, Reitz et al. 2003). The use of TSW resistant tomato, reflective mulch, insecticidal sprays, adjusting planting dates, and combinations of these tactics have had significant results on reducing TSW (Coutts and Jones 2005, Momol et al. 2004, Reitz et al. 2003, Riley and Pappu 2000, 2004). This study also demonstrated that the composition of thrips species in Georgia tomato is not consistent over years and would need to be assessed each year to determine the specific effectiveness of thrips control tactics.

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References Cited

Accotto, G. P., G. Nervo, N. Acciarri, L. Tavella, M. Vecchiati, M. Schiavi, G. Mason and A. M. Vaira. 2005. Field evaluation of tomato hybrids engineered with *Tomato spotted wilt virus* sequences for virus resistance, agronomic performance, and pollen-mediated transgene flow. Phytopathology 95: 800-807.

Best, R. J. 1968. Tomato spotted wilt virus, Pg. 65-146. *In* Smith, K.M. and M.A. Lauffer (eds), Advances in Virus Res., Vol. 13. Academic Press, NY.

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

Coutts, B. A. and R. A. C. Jones. 2005. Suppressing spread of Tomato spotted wilt virus by drenching infected source or healthy recipient plants with neonicatinoid insecticides to control thrips vectors. Ann. Appl. Biol. 146: 95-103.

Fonsah, E. G., C. M. Ferrer, D. G. Riley, S. Sparks and D. Langston. 2010. Cost and benefit analysis of Tomato spotted wilt virus (TSWV) management technology in Georgia. The Southern Agric. Econ. Assoc. Conf. (SAEA). http://ageconsearch.umn.edu/bitstream/56386/2/51028.pdf.

Gitaitis, R. 2009. Tospoviruses in Georgia vegetables, Pg. 24-27. *In* Tospoviruses in Solanaceae and other crops in the coastal plain of Georgia. Univ. of Georgia, Coll. Agric. Envir. Sci. Res. Bull. 1354.

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

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

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

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

Joost, P. H. and D. G. Riley. 2004. Sampling techniques for thrips (Thysanoptera: Thripidae) in pre-flowering tomato. J. Econ. Entomol. 97: 1450-1454.

Kirk, W. D. J. 1984. Pollen feeding in thrips (Insecta: Thysanoptera). J. Zool. 204: 107-117.

Kirk, W. D. J. 1985. Pollen-feeding and the host specificity and fecundity of flower thrips (Thysanoptera). Ecol. Entomol. 10: 281-289.

Kirk, W. D. J. 1997. Distribution, abundance, and population dynamics. Pg. 217-258. *In* T. Lewis, (ed.) Thrips as Crop Pests. CAB International, Wallingford, UK.

Lewis, T. 1997. Flight and dispersal, Pg. 175-196. *In* T. Lewis, (ed.) Thrips as Crop Pests. CAB International, Wallingford, UK.

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

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

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

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

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

Oetting, R. D., R. J. Beshear, T. X. Liu, S. K. Braman and J. R. Baker. 1993. Biology and identification of thrips on greenhouse ornamentals. Georgia Agric. Exper. Station Res. Bull. 414, 20 pp.

Olatinwo, R., G. Hoogenboom, T. Prabhakaran, J. O. Paz and D. Riley. 2010. The Weather Research and Forecasting (WRF) model: Application in prediction of thrips populations. J. Appl. Entomol. 135: 81-90.

Olson, S. M. 2009. Physiological, nutritional, and other disorders of tomato fruit. HS-954, Univ. Florida, Gainesville.

Persley, D. M., J. E. Thomas and M. Sharman. 2006. Tospoviruses - an Australian perspective. Australas. Plant Pathol. 35: 161-180.

Peters, D., F. Wijkamp, F. van de Wetering and R. Goldbach. 1996. Vector relations in the transmission and epidemiology of tospoviruses. Acta Hortic. 431: 29-43.

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

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

Riley, D. G. and H. Pappu. 2004. Tactics for management of thrips (Thysanoptera: Thripidae) and *Tomato Spotted Wilt Tospovirus* in tomato. J. Econ. Entomol. 97: 1648-1658.

Riley, D. G., A. Chitturi and A. N. Sparks Jr. 2007. Does natural deposition of pine pollen affect the ovipositional behavior of *Frankliniella occidentalis* and *Frankliniella fusca* (Thysanoptera: Thripidae)? Entomol. Exp. Appl. 124: 133-141.

Riley, D. G., G. M. Angelella and R. M. McPherson. 2010. Pine pollen dehiscence relative to thrips (Thysanoptera: Thripidae) population dynamics. Entomol. Exp. Appl. 138: 223-233.

Riley, D. G., S. V. Joseph, R. Srinivasan and S. Diffie. 2011. Thrips vectors of tospoviruses. J. Integ. Pest Mngmt. 2(1): 1-10.

Sargent, S. A. and C. L. Moretti. 2004. The commercial storage of fruits, vegetables, and florist and nursery stocks: tomato. USDA, ARS Agriculture handbook 66. (http://www.ba.ars.usda.gov/hb66/138tomato.pdf).

SAS Institute. 2003. User's manual, version 9.1 SAS Institute, Cary, NC.

Stannard, L. J. 1968. The Thrips, or Thysanoptera of Illinois. Illinois Nat. His. Surv. Bull. 29: 215-552.

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

Ullman, D. E., J. L. Sherwood and T. L. German. 1997. Thrips as vectors of plant pathogens, Pg. 539-565. *In* T. Lewis, (ed.) Thrips as Crop Pests. CAB International, Wallingford, UK.

Wijkamp, I., N. Almarza, R. Goldbach and D. Peters. 1995. Distinct levels of specificity in thrips transmission of tospoviruses. Phytopathology 85: 1069-1074.

Wijkamp, I., R. Goldbach and D. Peters. 1996. Propagation of Tomato spotted wilt virus in *Frankliniella occidentalis* does neither result in pathological effects nor in transovarial passage of the virus. Entomol. Exp. Appl. 81: 285-292.