Overwintering Viruliferous *Frankliniella occidentalis* (Thysanoptera: Thripidae) as an Infection Source of *Tomato spotted wilt virus* in Green Pepper Fields

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ABSTRACT

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Populations of overwintering viruliferous *Frankliniella occidentalis* were evaluated in *Tomato spotted wilt virus* (TSWV)-affected green pepper fields in Bungo-Ohno City, Oita Prefecture, Japan. A survey of TSWV-infected weeds showed that the incidence of infection was low in weeds. *Stellaria aquatica* was infected frequently; however, the infections were considered secondary cases since *S. aquatica* appeared in the fields around late February to early March. In contrast, TSWV was frequently detected from green pepper fruits until they rotted. *F. occidentalis* primarily inhabited and reproduced on the green pepper fruits and moved to *Lamium amplexicaule* when the fruits rotted and subsequently spread to other weed species as young shoots or flowers appeared. The flying activity level of *F. occidentalis* rose in late February, and viruliferous *F. occidentalis* transmitted TSWV to green pepper plants. We concluded that TSWV-infected green pepper fruits discarded in greenhouses and fields are the major source of infection.

Additional keywords: sticky trap

Tomato spotted wilt virus (TSWV) is a serious pathogen affecting a wide range of vegetable and ornamental crops around the world. The spotted wilt disease caused by TSWV was first reported on tomato plant in Australia (3,19). In Japan, TSWV was first isolated from *Dahlia pinnata* in 1965 (20) and subsequently isolated from tomato (10), green pepper, and many other ornamental crops (9). TSWV rapidly spread throughout Japan in the late 1990s and became one of the most serious pathogens of vegetables and ornamental crops grown in greenhouses.

TSWV is the type species of the genus *Tospovirus* in the family *Bunyaviridae* (17). This pathogen is transmitted by at least seven thrips species (16) that are members of the family *Thripidae*. *Frankliniella occidentalis* (Pergande) was first

found in 1992 and currently is one of the common species in greenhouses in Japan. Since the distribution of *F. occidentalis* and epidemics of TSWV disease are correlated, it is considered that *F. occidentalis* is involved in the prevalence of TSWV-induced diseases in Japan. The life cycle of *F. occidentalis* is 12.1 days at 25.0°C (8). In most cases, its population peaks in the summer. However, reproduction is hampered above 35°C. *F. occidentalis* can survive for 30 days at -5°C under experimental conditions (7). Field experiments in the southeastern United States revealed that *F. occidentalis* can overwinter in the fields and reproduce throughout the winter (1,4,5).

Thrips and weeds play important roles in the infection cycles of TSWV in fields. In particular, thrips on TSWV-infected weeds appeared to cause primary infection in the spring. McPherson et al. (13) surveyed the presence of viruliferous thrips on weeds in TSWV-infected tobacco fields during the winter and revealed that several weed species were infected with TSWV and *F. occidentalis* and *F. fusca* on weeds could be potential vectors in tobacco fields. Similarly, Groves et al. (6) revealed that three annual weed species were infected with TSWV from winter to spring and were potential sources of infection.

In Bungo-Ohno City, Oita Prefecture, Japan, where green peppers are extensively cultivated from early spring to autumn, TSWV-induced diseases have been common since the first outbreak in 1998. Economic loss due to TSWV-induced diseases in this city was more than \$180,000 a year. In this area, *F. occidentalis* is the dominant thrips species in greenhouses and is considered to be the major vector of TSWV. It would be an effective control measure if we could break the infection cycle during the winter; however, the ecological characteristics of overwintering thrips and weeds in this area had been unclear. The objectives of this study were to estimate the seasonal transition of the infection potential by surveying populations of overwintering viruliferous *F. occidentalis* around green pepper greenhouses and investigating the incidence of TSWV infection in weeds in the winter.

MATERIALS AND METHODS

Survey locations. Two greenhouses in Koshiji (survey location A, [SLA]), Kamizono (SLB), and one open field, where a greenhouse had been assembled in the summer in Bungo-Ohno City in Kokuragi (SLC), were chosen for this study. Green peppers were grown in these greenhouses from the end of March to November, and TSWV had been detected from green pepper plants and *F. occidentalis* during the growing periods in 2002 and 2003, respectively (*unpublished data*). A green pepper greenhouse in Katashima that was not affected by TSWV (SLH) was chosen as a negative control.

Field survey of TSWV infection on weeds and green pepper fruits left in greenhouses. Weeds and green pepper fruits left at the survey locations were sampled in SLA, SLB, and SLC. TSWV infection was examined by reverse transcription-polymerase chain reaction (RT-PCR). RNA extraction and RT-PCR were performed using ISOGEN (Nippon gene, Tokyo, Japan) and GeneAmp Gold RNA PCR kit (Applied Biosystems, Foster City, CA), respectively, according to the manufacturer's protocols. Reverse transcription of RNA was conducted for 30 min at 42°C, and PCR was subsequently performed with

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40 cycles of 94°C for 30 sec, 50°C for 30 sec, and extension at 72°C for 1 min using a primer set designed to detect the TSWV *N* gene (TsN-5, 5' TTTAACAACACTAAG-CAAGCACA 3', corresponding to nucleotides 1,899-1,920 of GenBank accession no. D00645; and, TsS3, 5' GCTCTAGAG-CAATTGTGTCAATT 3', the reverse complement of nucleotides 2,916-2,899). RT-PCR products were fractionated on 1% agarose gels and observed under UV light after staining with ethidium bromide (50 µg/ml).

Field survey of viruliferous *F. occidentalis*. Weeds and green pepper fruits left in the survey locations were sampled every 6 to 25 days from November 2002 to March 2003 in SLA, and from January 2003 to May 2004 in SLB and SLC. *F. occidentalis* adults were collected from the weeds and green pepper fruits, and TSWV was detected by double-antibody sandwich

enzyme-linked immunosorbent assay (DAS-ELISA). TSWV-specific antibody and alkaline phosphatase conjugate antibody were obtained from the Japan Plant Protection Association (Tokyo). Absorbance values (A_{405}) were measured with an Immuno Reader NJ-2001 (Inter Med, Roskilde, Denmark). Samples were considered positive if they showed values three times higher than the mean of healthy female *F. occidentalis* adults.

Transition of *F. occidentalis* populations in the field. To estimate the inhabitation pattern of *F. occidentalis*, seven weed species and green pepper fruits were collected every 6 to 15 days from 9 January to 21 April 2004 in SLC. *F. occidentalis* adults were collected from the samples. Larvae were grown by feeding with broad beans (18) to identify the species.

Survey of viruliferous *F. occidentalis* transition using sticky traps. Blue sticky

traps (HORIVER, Arysta Life Science, Tokyo, Japan) were used to capture flying *F. occidentalis* in SLC. Three sticky traps were placed in each field approximately 30 cm high. Sticky traps were changed every 6 to 15 days from January 2003 to April 2004, and each adult insect was detached from the trap plate under microscope observation. Viruliferous *F. occidentalis* that was bonded on a sticky trap for 2 weeks can be distinctly differentiated from healthy ones by DAS-ELISA (K. Komi, M. Okuda, and T. Iwanami, unpublished data). Therefore, DAS-ELISA using TSWV-specific antibody and alkaline phosphatase conjugate antibody was conducted for each sample, and samples were considered viruliferous if A_{405} is three times more than the mean of healthy *F. occidentalis*.

Evaluation of natural infection using seedling traps. To evaluate the natural infection of TSWV in Bungo-Ohno City, green pepper seedlings (cv. Sarara) were grown in 10-cm-diameter pots and placed in SLC. On 7 April 2004, 10 82-day-old seedlings were planted 50 cm apart in the corner of a field. The seedlings were collected on 18 May 2004. TSWV infection was examined by DAS-ELISA.

RESULTS

TSWV infection in weeds and green pepper fruits. Seventy-seven plants of 14 weed species, 29 plants of 9 species, and 28 plants of 7 species were sampled in SLA, SLB, and SLC, respectively, and RT-PCR tests revealed that 3.9, 20.6, and 14.3% of the plants were TSWV infected, respectively (Table 1). However, the infected species were limited. A relatively high proportion of *Stellaria aquatica* was infected with TSWV. In contrast, TSWV was frequently detected from green pepper fruits left at each location until the fruits rotted away.

Field survey of viruliferous *F. occidentalis*. A field survey in SLA revealed that *F. occidentalis* adults inhabited green pepper fruits discarded on the ground until

Table 1. Tomato spotted wilt virus infection on weeds and discarded green pepper fruits

Hosts	Location ^a		
	SLA	SLB	SLC
Discarded green pepper fruits	11 (11) ^b	35 (37)	34 (41)
<i>Artemisia princeps</i>	0 (5)	0 (1)	... ^c
<i>Cerastium glomeratum</i>	0 (1)		0 (4)
<i>Conyza bonariensis/Conyza sumatrensis</i>	0 (5)	0 (1)	0 (2)
<i>Corydalis incisa</i>	...	...	0 (2)
<i>Galinsoga ciliata</i>	1 (14)	...	...
<i>Gnaphalium japonicum</i>	0 (10)	...	...
<i>Ixeris stolonifera</i>	0 (3)	...	...
<i>Lamium amplexicaule</i>	...	1 (7)	0 (4)
<i>Oxalis corniculata</i>	...	0 (1)	0 (1)
<i>Plantago asiatica</i>	0 (5)	...	...
<i>Portulaca oleracea</i>	0 (1)	...	...
<i>Rorippa islandica</i>	0 (2)	...	...
<i>Solanum nigrum</i>	1 (18)	0 (4)	...
<i>Sonchus oleraceus</i>	0 (1)	0 (1)	...
<i>Stellaria aquatica</i>	1 (8)	4 (5)	3 (9)
<i>Veronica persica</i>	0 (2)	1 (6)	1 (6)
<i>Vicia angustifolia</i>	0 (2)	0 (3)	...
Infection rate	3.9%	20.6%	14.3%

^a Survey periods were from 25 November 2002 to 12 March 2003 in Koshiji (greenhouse [SLA]) and from 1 March to 23 March 2004 in Kamizono (greenhouse [SLB]) and Kokuragi (open field [SLC])

^b Number of TSWV-infected samples. Number tested is indicated in parentheses.

^c ... = No plants were found.

Table 2. Population and viruliferous proportion of adult *Frankliniella occidentalis* on weeds and discarded green pepper fruits in a greenhouse in Koshiji

Hosts	2002				2003					
	11/12	11/26	12/12	12/24	1/8	1/23	2/10	2/25	3/11	3/25
Discarded green pepper fruits	25 (7) ^a	39 (14)	3 (2)	19 (3)	35 (18)	9 (4)	4 (4)	* ^b	*	*
<i>Solanum nigrum</i>	... ^c	...	1 (1)	6 (1)	4 (1)	3 (1)	...	...	...	...
<i>Cerastium glomeratum</i>	...	...	9 (3)	...	...	...	0 (0)	2 (2)	...	0 (0)
<i>Erigeron Canadensis</i>	...	...	...	...	3 (0)	...	...	6 (3)	4 (2)	...
<i>Gnaphalium pensylvanicum</i>	...	...	...	...	...	38 (15)	...	9 (3)	...	...
<i>Conyza sumatrensis</i>	...	...	...	...	...	...	4 (1)	...	...	...
<i>Stellaria aquatica</i>	...	...	...	...	...	...	6 (1)	0 (0)	7 (5)	...
<i>Gnaphalium japonicum</i>	...	...	...	...	...	...	...	15 (6)	...	...
<i>Vicia angustifolia</i>	...	...	...	...	...	...	...	1 (1)	...	...
<i>Artemisia princeps</i>	...	...	...	...	...	...	...	...	1 (0)	0 (0)
<i>Gnaphalium affine</i>	...	...	...	...	...	...	...	...	4 (2)	...
<i>Senecio vulgaris</i>	...	...	...	...	...	...	...	...	3 (1)	...
<i>Bothriospermum tenellum</i>	...	...	...	...	...	...	...	...	...	4 (2)

^a Number of adult *F. occidentalis* collected. Number of viruliferous thrips, which was identified by double-antibody sandwich enzyme-linked immunosorbent assay, is indicated in parentheses.

^b * = All fruits were decomposed completely.

^c ... = No samples were collected in the field.

they rotted in February (Table 2). *F. occidentalis* (15.8 to 100%) on the fruits were TSWV viruliferous. No fresh green pepper fruit was found after 25 February. *F. occidentalis* adults were captured from 12 wild weed species from 12 December to 25 March. Most samples were inhabited by viruliferous *F. occidentalis* occasionally. The proportion of viruliferous *F. occidentalis* did not decrease during the survey period, although the insects changed host plants. Similarly, a field survey in SLB showed that green pepper fruits discarded on the ground were inhabited by *F. occidentalis* until 1 March (Table 3). There

were viruliferous adults of *F. occidentalis* through the winter (25.0 to 66.7%) with the tendency to decrease gradually. In this field, there were very few weeds. Adults of *F. occidentalis* were captured from four wild weed species in March. Viruliferous *F. occidentalis* was detected from *S. aquatica* only on 8 March.

In an open field (SLC), decaying green pepper fruits remained until 23 February and *F. occidentalis* adults inhabited the fruits (Table 4). The green pepper fruits were decomposed completely by 1 March. Adults of *F. occidentalis* were captured from 10 wild weed species. Many *F. occi-*

dentalis were captured from the weeds, and 22.2 to 29.8% of the populations were viruliferous. No TSWV viruliferous thrips were found on either green pepper fruits or weeds in SLH through the winter, where TSWV had not been detected during the cultivation period in the summer (data not shown).

Transition of *F. occidentalis* populations in the field. The population analysis of *F. occidentalis* inhabiting the green pepper fruits and six weed species showed that adult and larval *F. occidentalis* inhabited green pepper fruits until 23 February (Table 5). No thrips were captured from

Table 3. Population and viruliferous proportion of adult *Frankliniella occidentalis* on weeds and discarded green pepper fruits in a greenhouse in Kamizono

Hosts	2004						
	1/9	2/10	2/23	3/1	3/8	3/17	3/23
Discarded green pepper fruits	5 (3) ^a	6 (4)	6 (1)	4 (1)	* ^b	*	*
<i>Stellaria aquatica</i>	... ^c	...	...	...	15 (3)	1 (0)	...
<i>Conyza sumatrensis</i>	...	...	...	...	...	4 (0)	...
<i>Corydalis incisa</i>	...	...	...	...	...	2 (0)	...
<i>Lamium amplexicaule</i>	...	...	...	...	...	...	1 (0)

^a Number of adult *F. occidentalis* collected. Percentages of viruliferous thrips are indicated in parentheses.

^b * = All fruits were decomposed completely.

^c ... = No samples were collected in the field.

Table 4. Population and viruliferous proportion of adult *Frankliniella occidentalis* on weeds and discarded green pepper fruits in an open field in Kokuragi

Hosts	2004									
	1/9	1/20	1/29	2/23	3/1	3/8	3/17	3/23	4/7	4/21
Discarded green pepper fruits	2 (0) ^a	3 (1)	9 (2)	47 (14)	* ^b	*	*	*	*	*
<i>Artemisia princeps</i>	... ^c	...	...	...	14 (2)	...	8 (0)	16 (4)	4 (2)	...
<i>Vicia angustifolia</i>	...	...	...	...	44 (5)	...	17 (5)	12 (3)	22 (4)	...
<i>Lamium amplexicaule</i>	...	...	...	...	195(25)	122(26)	...	29 (10)	17 (5)	...
<i>Viola mandshurica</i>	...	...	...	...	3 (0)	...	8 (3)	...	...	...
<i>Conyza sumatrensis</i>	...	...	...	...	...	...	7 (0)	...	...	...
<i>Sonchus oleraceus</i>	...	...	...	...	...	...	5 (0)	...	...	...
<i>Capsella bursa-pastoris</i>	...	...	...	...	...	...	35 (4)	14 (1)	...	...
<i>Stellaria aquatica</i>	...	...	...	...	...	...	17 (2)	6 (4)	15 (5)	...
<i>Veronica persica</i>	...	...	...	...	...	...	7 (1)	2 (1)	8 (2)	...
<i>Trifolium repens</i>	...	...	...	...	...	...	...	...	...	56 (5)

^a Number of adult *F. occidentalis* collected. Percentages of viruliferous thrips are indicated in parentheses.

^b * =All fruits were decomposed completely.

^c ... = No samples were collected in the field.

Table 5. Transition of adult and larval *Frankliniella occidentalis* population in an open field in Kokuragi

Hosts	Stage ^a	2004										
		1/9	1/20	1/29	2/10	2/23	3/1	3/8	3/17	3/23	4/7	4/21
Discarded green pepper fruits	Adult	0.1 ^b	0.3	0.7	1.6	1.5	0	... ^c	...	...	...	...
	Larvae	1.4	1.4	1.0	2.5	0.1	0	...	...	...	...	...
<i>Lamium amplexicaule</i>	Adult	...	...	...	0	2.7	4.9	2.6	4.2	3.9	0.5	0
	Larvae	...	...	...	0	0	0	0.1	2.8	0.5	0.2	0
<i>Vicia angustifoli</i>	Adult	...	...	...	0	0.3	0	0	5.7	2.0	2.2	0
	Larvae	...	...	...	0	0	0	0	4.0	0	2.7	0
<i>Artemisia princeps</i>	Adult	...	...	...	0	0.6	0	0	1.5	2.3	0.3	0
	Larvae	...	...	...	0	0	0	0	2.8	3.6	2.3	0
<i>Veronica persica</i>	Adult	...	...	...	...	0.3	0	0	0.7	0.2	0.8	0
	Larvae	...	...	...	...	0	0	0	1.4	2.4	6.2	0
<i>Stellaria aquatica</i>	Adult	...	...	...	...	...	0	0	0.9	2.6	0	0
	Larvae	...	...	...	...	...	0	0	3.0	5.8	0.3	0
<i>Capsella bursa-pastoris</i>	Adult	...	...	...	...	...	...	0	3.5	1.4	0.7	0
	Larvae	...	...	...	...	...	...	0	2.3	0.3	1.3	0
<i>Trifolium repens</i>	Adult	...	...	...	...	...	...	...	...	0	1.2	2.9
	Larvae	...	...	...	...	...	...	...	...	0	1.0	0.3

^a Larvae were bred with broad beans to identify as *F. occidentalis*.

^b Average number of thrips captured from a sample.

^c ... = No samples were collected in the field.

weeds until 10 February. As the weeds grew, *F. occidentalis* started to be detected from weeds. *F. occidentalis* adults were found mainly on *Lamium amplexicaule* but also *Vicia angustifolia*, *Artemisia princeps*, and *Veronica persica*. However, larvae did not appear until 8 March. After 17 March, adult and larval *F. occidentalis* spread on *S. aquatica* and *Capsella bursa-pastoris*. *F. occidentalis* was found on *Trifolium repens* on 21 April as the flowers bloomed.

Survey of flying viruliferous *F. occidentalis* using sticky traps. Sticky traps placed in SLC first captured *F. occidentalis* adults on 10 February. The number of *F. occidentalis* captured on the sticky traps peaked around 1 March and decreased gradually thereafter (Fig. 1). Percentages of viruliferous *F. occidentalis* did not significantly change (Fisher's exact test, $P = 0.8094$) while being trapped from 10 February to 7 April.

TSWV infection in seedling traps. On 18 May, 6 of 10 green pepper seedlings planted in SLC showed necrotic ringspot and yellowing, which are typical symptoms of TSWV infection. TSWV was detected from the symptomatic leaves by DAS-ELISA.

DISCUSSION

In this study, we evaluated populations of viruliferous *F. occidentalis* and TSWV-infected weeds in TSWV-affected green pepper fields to reveal the infection source of TSWV in the winter. Bungo-Ohno City is located in the center of Kyusyu, Japan. The climate is relatively mild and it rarely snows during the winter. In this area, sweet potato, taro, and tobacco are grown in fields and ornamental flowers, green pepper, and strawberry are grown in greenhouses. Green peppers are usually grown

from March to November, and any crops that could be infected with TSWV are not grown near the greenhouses when green pepper seedlings are planted in the early spring. However, green pepper plants, which were confirmed negative in the nursery, were infected with TSWV as soon as they were transplanted to the greenhouses.

Crude sap from some weeds gives a false positive reaction in ELISA. To avoid this problem, RT-PCR, which is less likely to give a false positive reaction, was conducted to test for TSWV infection in weeds in this study. Among a few weed species found in the greenhouses in the winter, some species were infected with TSWV. Comparatively, a high proportion of *S. aquatica* was infected. *S. media* was often reported as a reservoir of TSWV (2,6,14,15). However, infection of *S. aquatica* is considered secondary in this area because *S. aquatica* appears in the fields in late February or early March. Incidence of infection in other weed species was low. The results suggest that weeds represent only a minor source in this area. On the other hand, green pepper fruits discarded in the greenhouses and open fields were frequently infected with TSWV. Interestingly, TSWV was detected in the discarded green pepper fruits until March, even though the fruits matured and turned red. TSWV was also detected in *F. occidentalis* collected from the green pepper fruits. Larvae of *F. occidentalis* collected from these fruits were TSWV positive after being grown to adults by feeding on healthy broad beans (data not shown). This suggests that *F. occidentalis* feeding on the TSWV-infected green pepper fruits acquired and could transmit TSWV to green pepper seedlings.

Population analysis showed that *F. occidentalis* primarily inhabited and reproduced on the green pepper fruits and moved to *L. amplexicaule* when the fruits rotted and subsequently spread to other weed species as young shoots or flowers appeared. The flying activity level of *F. occidentalis* rose in late February and more than 15.4% of *F. occidentalis* was viruliferous. Seedling traps suggested that the viruliferous *F. occidentalis* transmitted TSWV to green pepper plants in this area. Several weed species were inhabited by *F. occidentalis* in greenhouses and fields. However, rare TSWV infections of weeds in this area suggest movement of the viruliferous thrips from TSWV-infected green pepper to weeds. Another bit of circumstantial evidence is that TSWV was not detected from some host plants despite the presence of viruliferous *F. occidentalis* (data not shown). Although some weeds were inhabited by *F. occidentalis* during the winter, as reported previously (11,13,14), *F. occidentalis* showed clear preference to green pepper fruits until the fruits rotted. Maris et al. suggested that TSWV-infected plants significantly attract *F. occidentalis* (12). The preference for TSWV-infected green pepper fruits was so strong that the population of *F. occidentalis* in this area might be biased. Further study will be needed to clarify the impact to the population.

In this study, we concluded that TSWV-infected green pepper fruits discarded in greenhouses and fields are the major source of infection in this area. The occurrence of TSWV disease in Bungo-Ohno City drastically fell during 2005 after green pepper fruits of the previous season were entirely removed from TSWV-affected greenhouses (data not shown). This study shows that we can terminate the infection cycle if we eliminate the source of TSWV infection.

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Fig. 1. Transition of number of *Frankliniella occidentalis* and percentage of viruliferous individuals captured with sticky traps. Columns indicate the number of insects captured on the traps (left scale). Values are the average of three traps, and the vertical bar above each column indicates standard deviation. The solid line indicates percentage of viruliferous *F. occidentalis* (right scale).

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