

Life Cycle-Based Host Range Analysis for Tomato Spotted Wilt Virus in Korea

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Tomato spotted wilt virus (TSWV) is one of the plant viruses transmitted by thrips and causes severe economic damage to various crops. From 2008 to 2011, to identify natural host species of TSWV in South Korea, weeds and crops were collected from 5 regions (Seosan, Yesan, Yeonggwang, Naju, and Suncheon) where TSWV occurred and were identified as 1,104 samples that belong to 144 species from 40 families. According to reverse transcription-polymerase chain reaction, TSWV was detected from 73 samples from 23 crop species, 5 of which belonged to family Solanaceae. Additionally, 42 weed species were confirmed as natural hosts of TSWV with three different life cycles, indicating that these weed species could play an important role as virus reservoirs during no cultivation periods of crops. This study provides up-to-date comprehensive information for TSWV natural hosts in South Korea.

Keywords : reservoir, Tomato spotted wilt virus (TSWV), *Tospovirus*

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Tomato spotted wilt virus (TSWV) is a member of the genus *Orthotospovirus* in the family *Tospoviridae* (Maes et al., 2018). Their genome consists of three negative or ambisense, single-stranded RNA species designated as S (2.9 kb), M (4.8 kb), and L (8.9 kb) with partially complementary terminal sequences (Adkins, 2000). Their pleomorphic particles are 80-120 nm in diameter with surface projections composed of two viral glycoproteins G1 and G2 (Adkins, 2000; Pappu, 2008). The first report of the disease ‘spotted wilt of tomato’ was described by Charles Brittlebank, an Australian phytopathologist, in 1919 (Best, 1968; Brittlebank, 1919). In 1930, Samuel characterized this pathogen as a virus and named it TSWV (Samuel, 1930). According to the first report of International Committee on Taxonomy of Viruses (ICTV), TSWV was the sole member of ‘Tomato spotted wilt virus group’ (Fenner, 1976). After the early 1990s, because several similar viruses to TSWV were identified and characterized, the genus *Tospovirus* was created and changed to the family *Tospoviridae* according to the most recently proposed classification (Maes et al., 2018; Murphy et al., 1995).

TSWV-infected plants show typical symptoms such as yellowing; mottling; chlorotic, ring spots of leaves and fruits; and stunting, inducing significant crop losses. Expression of these symptoms can vary depending on strain (or isolate) of the infected TSWV, plant species, crop cultivars and growth stage of the infected plants and environmental conditions of the infected plants (Adkins, 2000; German et

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al., 1992; Riley et al., 2011; Scholthof et al., 2011). TSWV is transmitted by approximately 10 species of thrips including the western flower thrips (*Frankliniella occidentalis*) (Riley et al., 2011; Sundaraj et al., 2014). TSWV occurrences have economic importance in cultivation of many crops because of the significantly decreased crop yields of the infected plants. In addition, TSWV disease spread rapidly to new healthy plants since viruliferous western flower thrips (*F. occidentalis*) are difficult for population management using chemical insecticides or natural organic compounds (Adkins, 2000; Jiang et al., 2017). Mechanical transmission of TSWV is also possibly transmitted from sap of naturally infected plants (Parrella et al., 2003).

TSWV is one of the plants viruses with the largest host range (Parrella et al., 2003). Over 1,000 plant species in over 85 families including many cultivated crops such as peanut (*Arachis hypogaea*), pepper (*Capsicum annuum*), potato (*Solanum tuberosum*), spinach (*Spinacia oleracea*), tobacco (*Nicotiana tabacum*), and tomato (*Solanum lycopersicum*) are reported TSWV natural hosts (Brittlebank, 1919; Cho et al., 1987; Costa, 1941; German et al., 1992; Parrella et al., 2003; Sakimura, 1940; Sherwood et al., 2009; Smith, 1931). In addition to economic crops, various weeds are also known natural hosts of TSWV and can be act as reservoirs for viral spread to other susceptible crops (Chatzivassiliou et al., 2001; Cho et al., 1986; Parrella et al., 2003).

TSWV is one of the most important plant viruses, reported in about 100 countries on all continents (OEPP/EPPO, 1999). In South Korea, TSWV was first reported on sweet pepper (paprika) from Yesan in 2004 (Kim et al., 2004) and spread nationwide. Mainly, TSWV occurrences in Korea have been reported continuously from tomato, pepper, and potato (Yoon et al., 2017). TSWV infection was also found in soybean (*Glycine max*), *Brugmansia suaveolens*, *Eustoma grandiflorum*, *Hoya carnosa*, *Humulus japonicas*, and *Peperomia obtusifolia* in Korea (Choi et al., 2014; Kim et al., 2018; Yoon et al., 2017, 2018a, 2019). Many hot pepper farms in Korea have suffered from TSWV.

Previously, the host range investigations of TSWV in various plants including weeds were reported (Cho et al., 1986, 1987; Parrella et al., 2003). In recent years, however, report from large-scale investigations have not been issued. In this study, to update lists, we examined crop and weed hosts of TSWV in Korea.

Materials and Methods

Sample collection. From 2008 to 2011, to investigate the



Fig. 1. Korean collection locations of crop and weed samples in this study.

influence of host plants on the spread of TSWV, samples of crops and weeds were collected. To investigate natural host plants from plants with different life cycles, plant samples were collected in the winter (November to February), spring (March to May), and summer (June to October). Sampling was conducted in five areas where occurrence of TSWV has been reported continuously (Suncheon, Naju, Yeonggwang, Seosan, and Yesan) in South Korea (Fig. 1). Sample collection points were inside and outside of non-heated greenhouses that had been used as nurseries for hot pepper seedlings, and other crop cultivating greenhouses or open fields around hot pepper cultivating greenhouses or open fields.

RNA isolation and virus diagnosis. Total RNA was extracted from collected samples with easy-spin Total RNA Extraction Kit (Intron Biotechnology, Seongnam, Korea) according to the manufacturer's manual. TSWV infection was confirmed by RT-PCR with AMV Reverse Transcriptase (for cDNA synthesis, Promega, Madison, WI, USA), GoTaq DNA Polymerase (for PCR, Promega), and

Table 1. Numbers of tested crops and weeds for *Tomato spotted wilt virus* (TSWV) detection in this study

Family	No. of tested species	No. of detected species	No. of tested samples
Asteraceae	29	9	300
Amaranthaceae	5	2	103
Apiaceae	2	1	13
Asclepiadaceae	1	1	4
Boraginaceae	1	0	1
Brassicaceae	9	8	80
Campanulaceae	1	1	4
Cannabaceae	1	0	3
Caprifoliaceae	1	0	1
Caryophyllaceae	6	6	104
Chenopodiaceae	4	2	46
Commelinoideae	1	1	18
Convolvulaceae	3	2	42
Crassulaceae	1	1	1
Cucurbitaceae	4	3	18
Euphorbiaceae	2	1	18
Fabaceae	12	7	36
Fagaceae	1	0	1
Lamiaceae	4	2	9
Liliaceae	6	2	38
Malvaceae	2	2	8
Meliaceae	1	0	7
Menispermaceae	1	0	1
Moraceae	3	1	10
Oleaceae	1	1	3
Oxalidaceae	3	0	4
Phytolaccaceae	1	1	60
Poaceae	8	1	56
Polygonaceae	4	1	11
Portulacaceae	1	0	4
Pteridaceae	1	0	1
Ranunculaceae	2	0	2
Rosaceae	3	0	9
Rubiaceae	2	2	16
Rutaceae	1	0	2
Scrophulariaceae	3	1	18
Solanaceae	8	6	37
Ulmaceae	1	0	3
Urticaceae	2	0	6
Vitaceae	2	0	6
	144	65	1,104

a TSWV-specific primer set (TSWV-6F, 5'-GAGATTCT-CAGAATCCCGAGT-3'; TSWV-6R, 5'-AGAGCAATC-GTGTC AATTTTATTC-3'), as described in a previous study (Tables 1-3) (Ko et al., 2013).

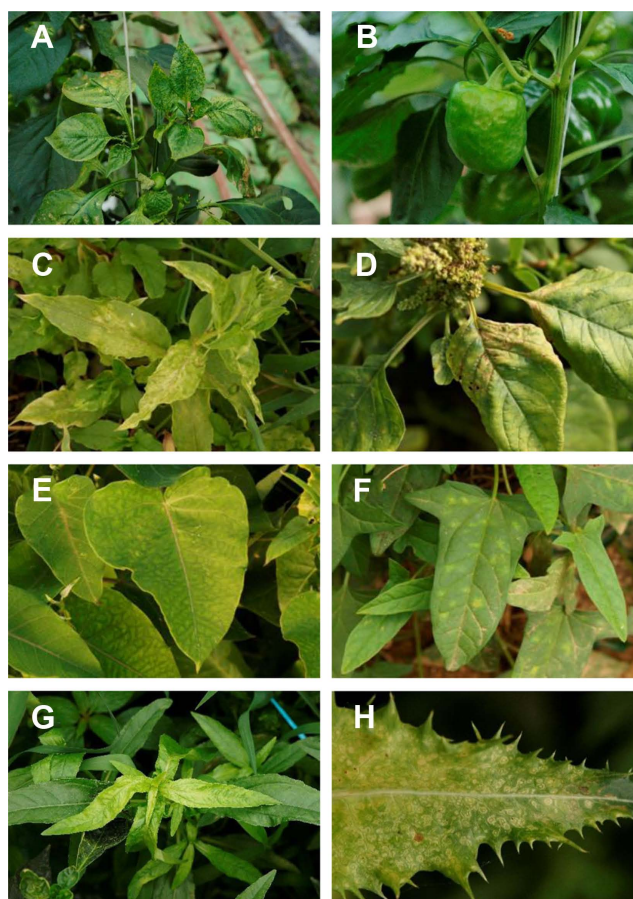


Fig. 2. *Tomato spotted wilt virus* (TSWV)-infected pepper plants and weeds collected for TSWV detection. (A) Leaf symptoms of TSWV-infected pepper plants. (B) Fruit symptoms of TSWV-infected sweet pepper plants. (C) *Stellaria aquatica*. (D) *Amaranthus lividus*. (E) *Metaplexis japonica*. (F) *Calystegia sepium*. (G) *Eclipta alba*. (H) *Sonchus asper*.

Results and Discussion

Species identification of collected samples. For 4 years, to identify natural hosts of crops and weeds that can be infected with TSWV, a total of 1,104 samples was collected from weeds (830 samples) and crops (274 samples) from five areas in Korea where TSWV has occurred (Table 1, Fig. 2). Because weeds have various life cycles (summer annual, winter annual, and perennial), it is hard to find many different kinds of weeds if sampling is conducted at a certain time only, so sample collections were done repeatedly in the different seasons. In addition, we sampled in the open fields, heated greenhouses, and non-heated greenhouses as the weed species that can be identified can vary depending on heating during winter. Collected samples were confirmed as belonging to 144 species (34 crops and

Table 2. Infection rate of *Tomato spotted wilt virus* (TSWV) in crops

Family	Species		No. of samples		Infectivity (%)
	Common name	Scientific name	Tested	Detected	
Apiaceae	Carrot	<i>Daucus carota</i>	1	0	0
	Dropwort	<i>Oenanthe javanica</i>	12	2	16.7
Asteraceae	Chrysanthemum	<i>Chrysanthemum morifolium</i>	21	4	19
	Crown daisy	<i>Chrysanthemum coronarium</i>	2	2	100
	Lettuce	<i>Lactuca sativa</i>	38	2	5.3
Brassicaceae	Chinese cabbage	<i>Brassica campestris</i>	22	17	77.3
	Chinese radish	<i>Raphanus sativus</i>	4	1	25
Campanulaceae	Bellflower root	<i>Platycodon grandiflorum</i>	1	1	100
Chenopodiaceae	Spinach	<i>Spinacia oleracea</i>	38	2	5.3
Convolvulaceae	Sweet potato	<i>Ipomoea batatas</i>	5	2	40
Cucurbitaceae	Cucumber	<i>Cucumis sativus</i>	9	3	33.3
	Oriental melon	<i>Cucumis melo</i>	1	1	100
	Pumpkin	<i>Cucurbita moschata</i>	7	0	0
Fabaceae	Cassia seed	<i>Cassia tora</i>	2	0	0
	Cow pea	<i>Vigna sinensis</i>	1	0	0
	Mung bean	<i>Phaseolus radiatus</i>	1	0	0
	Pea	<i>Pisum sativum</i>	2	2	100
	Peanut	<i>Arachis hypogaea</i>	18	5	27.8
Lamiaceae	Red bean	<i>Phaseolus angularis</i>	4	2	50
	Perilla seed	<i>Perilla frutescens</i>	2	0	0
Liliaceae	Chinese Chive	<i>Allium tuberosum</i>	5	0	0
	Shallot	<i>Allium ascalonicum</i>	24	6	25
	Spring onion	<i>Allium fistulosum</i>	5	0	0
	Wild chive	<i>Allium monanthum</i>	2	0	0
Malvaceae	Curled mallow	<i>Malva verticillata</i>	7	2	28.6
Moraceae	Mulberry tree	<i>Morus alba</i>	8	1	12.5
Pedaliaceae	Sesame	<i>Sesamum indicum</i>	3	1	33.3
Ranunculaceae	Peony root	<i>Paeonia lactiflora</i>	1	0	0
Rosaceae	Strawberry	<i>Fragaria ananassa</i>	1	0	0
Solanaceae	Eggplant	<i>Solanum melongena</i>	4	3	75
	Hot pepper	<i>Capsicum annuum</i>	12	6	50
	Potato	<i>Solanum tuberosum</i>	4	1	25
	Sweet pepper	<i>Capsicum annuum</i>	6	6	100
	Tomato	<i>Solanum lycopersicum</i>	1	1	100
Total			274	73	-

110 weeds) (Tables 1-3, Fig. 2).

Crop hosts. Among crops, plants that belong to the family Solanaceae including tomato, eggplant, and sweet pepper showed high infection rates (75-100%) (Table 2). In the family Liliaceae, on the other hand, infection was observed only in shallot (*Allium × proliferum*). According to our observation in Yesan, shallot was cultivated in a non-heated greenhouse during winter as a perennial crop and was confirmed as an important host for propagation of west-

ern flower thrips (*F. occidentalis*). Thus, TSWV-infected shallot is a natural host for TSWV overwintering and propagation of the insect vector. In the family Fabaceae, three species (pea, peanut, and red bean) were confirmed as natural hosts in some places collected from an open field in Yeonggwang near many chrysanthemum cultivating greenhouses. From those farms, TSWV was also detected from chrysanthemum (19%), and large colonies of western flower thrips were observed. Based on this result, the TSWV insect vector (western flower thrips), which cannot

overwinter in open fields (Brødsgaard, 1993), could directly damage the crops in the open field the next spring after overwintering in Chrysanthemum greenhouses. Tomato, eggplant (*S. melongena*), lettuce (*Lactuca sativa*), and crown daisy (*Glebionis coronaria*) were infected as seedling stages of the crops in nurseries with TSWV-infected hot pepper plants in Seosan.

Our results show that cooperation of thrips controls at neighboring farms is very important for effective TSWV control. In particular, the occurrence of the thrips in crops other than pepper, known as the most important host of TSWV, can be overlooked, but it is important because it can cause the spread of the thrips. In Korea, especially when farming scale is small, many kinds of crops are mixed and grown in other fields. As our results show, not only solanaceous crops but also beans, cucurbits, sesame, shallot, and curled mallow can be natural hosts of TSWV in South Korea. Since these are commonly grown crops in Korea, even if the pepper or tomato farmers manage thrips, it is very likely that viruliferous thrips including the western flower thrips (*F. occidentalis*) will continuously inflow from neighboring farms they are growing. This is also one of the reasons why TSWV problems continue to occur in Korea.

Weed hosts. Table 3 shows infection rates of TSWV in weeds. Among the weeds collected in areas of TSWV occurrence (110 species), 42 species in 22 families were identified as TSWV-infected. Asteraceae, Brassicaceae, and Caryophyllaceae families had the largest numbers of infected species (6 species each). According to life cycle analyses of TSWV weed hosts, 18 species were confirmed as winter annual (42.9%), 30.9% (13 species) were summer annual, and 26.2% (11 species) were perennial (Table 3, Fig. 3). Among the weeds analyzed from numerous (>20) samples, most samples of summer annual *Eclipta alba* (Fig. 2G) showed TSWV infection (95.6%), and half of winter annual *Stellaria media* (55%) and perennial *S. aquatica* (54.5%) (Fig. 2C) samples were confirmed as TSWV infected. A larger number of winter annual weeds were confirmed as many of those species overwintered in heated greenhouses in TSWV occurrence areas. These results suggest that winter annual weeds play important roles in overwintering of TSWV. From our previous study on overwintering of Tomato yellow leaf curl virus (TYLCV), it has been shown that *S. aquatica* can act as a viral source to newly introduced insect vectors in the next cultivation after overwintering in the non-heated greenhouse (Kil et al., 2015). We did not confirm overwintering of TSWV in wintering *S. aquatica* plants by time-course follow-up and arti-

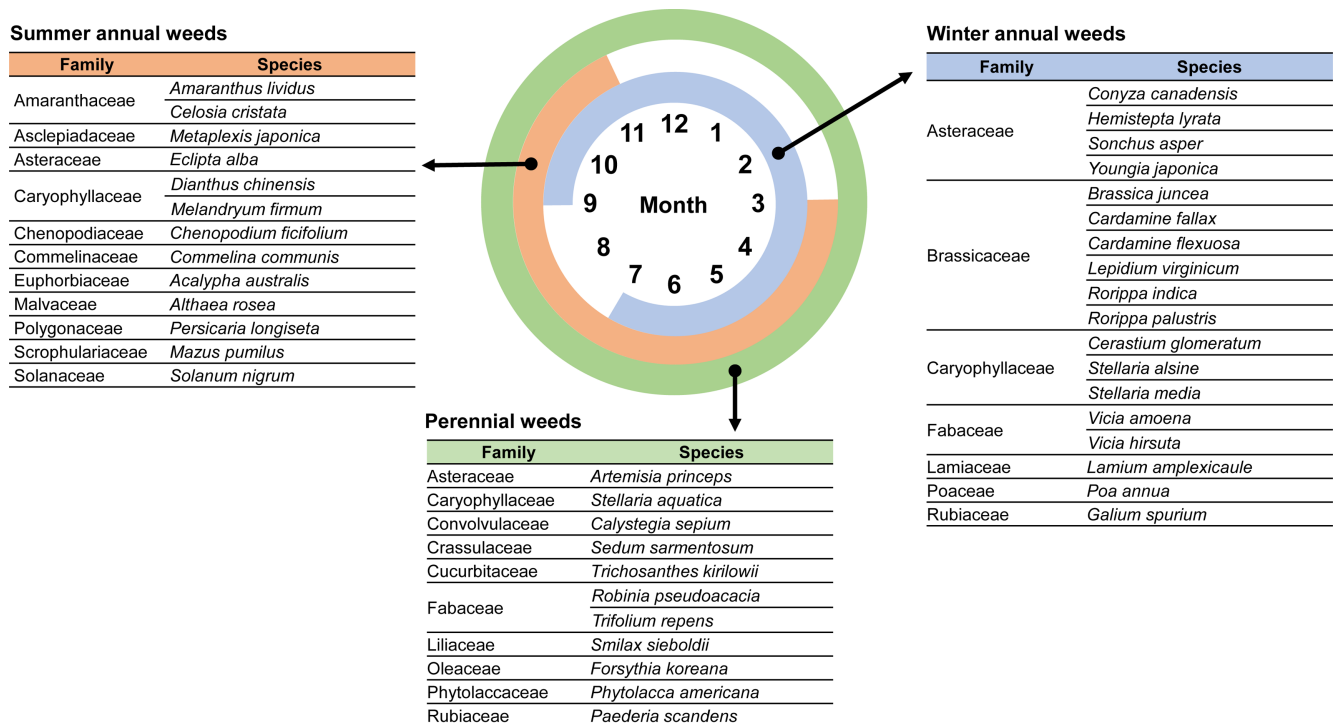


Fig. 3. Schematic diagram of Tomato spotted wilt virus (TSWV) life cycles in natural weed hosts. The three different circles indicate the three different life cycles (summer annual, winter annual, and perennial) of weed hosts introduced in this study.

Table 3. Infection rate of *Tomato spotted wilt virus* (TSWV) in detected weeds

Family	Species	Life cycle	No. of samples		Infectivity (%)
			Tested	Detected	
Amaranthaceae	<i>Amaranthus lividus</i>	SA	88	18	20.5
	<i>Celosia cristata</i>	SA	1	1	100
Asclepiadoideae	<i>Metaplexis japonica</i>	SA	4	1	25
Asteraceae	<i>Artemisia princeps</i>	P	50	17	34
	<i>Eclipta alba</i>	SA	45	43	95.6
	<i>Conyza canadensis</i>	WA	7	2	28.6
	<i>Hemistepta lyrata</i>	WA	14	6	42.9
	<i>Sonchus asper</i>	WA	17	11	64.7
	<i>Youngia japonica</i>	WA	12	4	33.3
	Brassicaceae	<i>Brassica juncea</i>	WA	2	1
<i>Cardamine fallax</i>		WA	4	2	50
<i>Cardamine flexuosa</i>		WA	29	2	6.9
<i>Lepidium virginicum</i>		WA	1	1	100
<i>Rorippa indica</i>		WA	1	1	100
<i>Rorippa palustris</i>		WA	3	1	33.3
Caryophyllaceae	<i>Cerastium glomeratum</i>	WA	8	2	25
	<i>Dianthus chinensis</i>	SA	2	2	100
	<i>Melandryum firmum</i>	SA	1	1	100
	<i>Stellaria alsine</i>	WA	2	2	100
	<i>Stellaria aquatica</i>	P	22	12	54.5
	<i>Stellaria media</i>	WA	69	33	55
Chenopodiaceae	<i>Chenopodium ficifolium</i>	SA	2	1	50
Commelinoideae	<i>Commelina communis</i>	SA	18	6	33.3
Convolvulaceae	<i>Calystegia sepium</i>	P	25	5	20
Crassulaceae	<i>Sedum sarmentosum</i>	P	1	1	100
Cucurbitaceae	<i>Trichosanthes kirilowii</i>	P	1	1	100
Euphorbiaceae	<i>Acalypha australis</i>	SA	17	1	5.9
Fabaceae	<i>Robinia pseudoacacia</i>	P	3	1	33.3
	<i>Trifolium repens</i>	P	1	1	100
	<i>Vicia amoena</i>	WA	1	1	100
	<i>Vicia hirsuta</i>	WA	1	1	100
	<i>Lamium amplexicaule</i>	WA	2	2	100
Lamiaceae	<i>Smilax sieboldii</i>	P	1	1	100
Malvaceae	<i>Althaea rosea</i>	SA	1	1	100
Oleaceae	<i>Forsythia koreana</i>	P	3	2	66.7
Phytolaccaceae	<i>Phytolacca americana</i>	P	60	16	26.7
Poaceae	<i>Poa annua</i>	WA	21	1	4.8
Polygonaceae	<i>Persicaria longiseta</i>	SA	5	1	20
Rubiaceae	<i>Galium spurium</i>	WA	12	8	66.7
	<i>Paederia scandens</i>	P	4	3	75
Scrophulariaceae	<i>Mazus pumilus</i>	SA	15	9	60
Solanaceae	<i>Solanum nigrum</i>	SA	6	1	16.7
Total			582	227	-

SA, summer annual; P, perennial; WA, winter annual.

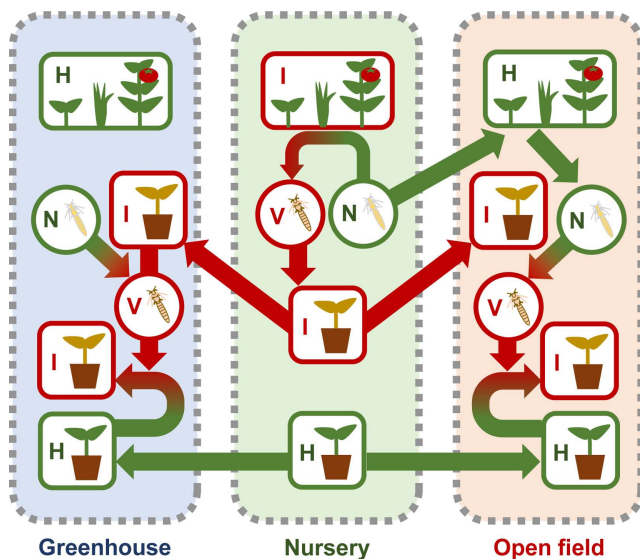


Fig. 4. Schematic diagram of *Tomato spotted wilt virus* (TSWV) disease cycles with thrips in a nursery for seedlings and greenhouse and open field for cultivating pepper plants. H, healthy plants; I, infected plants; N, non-viruliferous thrips; and V, viruliferous thrips.

ficial experiments shown in the previous study on TYLCV, but it can be inferred that *S. aquatica* plants infected with TSWV play a similar role in overwintering and spread. *S. media* showed the highest infectivity among winter annual weeds, is the dominant species in greenhouses in the winter season, and had a vital role as a reservoir host for TSWV and a main host for western flower thrips. Perennial weeds including *Artemisia princeps*, *S. aquatica*, *Calystegia sepium* (Fig. 2F), and *Phytolacca americana* are common in cultivation areas in Korea, so it is likely that they can act as green bridges for TSWV.

Epidemiological aspects of TSWV infection in crops and weeds in Korea. TSWV occurs repeatedly through complex interactions between main host plants, other crop and weed hosts, and the insect vector thrips in Korea (Fig. 4). In hot pepper cultivating farms and nurseries, TSWV occurrence is common in Korea. The western flower thrips has spread to all areas of Korea. As shown in the above results, weeds growing in a cultivation area and other crops grown in the same or neighboring greenhouses also can be infected with TSWV and weeds act as intermediate hosts. In a nursery for hot pepper seedlings in spring, TSWV infection was detected from *Cetastium glomeratum*, *S. aquatica*, *S. media*, *Lamium amplexicaule*, and *Galium spurium*, which are winter annual or perennial weeds. If healthy plants are moved to an open field or greenhouse for cultivation, some viruliferous insect vector can infect

them, creating additional inoculum for another vector. To overcome this cycle, control of insect vectors and weeds is necessary, and selection of TSWV-resistant cultivars can reduce economic damage. However, there have been a few reports for TSWV isolates that overcome *Tsw* gene-mediated resistance in pepper (Boiteux and de Ávila, 1994; Jiang et al., 2017; Riley et al., 2011).

TSWV has been a long-standing problem in over 100 countries, and its host range is the largest (Cho et al., 1986, 1987; Parrella et al., 2003). In Korea, TSWV has been indigenous as a representative plant virus that continuously damages pepper cultivation, and it is damaging not only peppers but also cultivation of tomatoes, potatoes and chrysanthemums. In addition to the known hosts, new hosts are also being reported in Korea. *H. japonicas*, one of weeds that are easily observed in farms, was reported as TSWV-infected (Yoon et al., 2018a). Soybean (*Glycine max*) cultivated commonly and famous ornamental plant *P. obtusifolia* introduced from Taiwan and China have also been identified as TSWV recently (Yoon et al., 2018b, 2019). These reports mean that TSWV host range analyses for the commonly cultivated or newly introduced crops, and the weeds found on farms should be done continuously to update lists of TSWV hosts, which can be helpful to design strategy for effective controls. This study was conducted to investigate crop and weed hosts of TSWV from areas near hot pepper cultivating farms in Korea and 23 crop species and 42 weed species were confirmed as TSWV-infected in fields. Our updated list of natural hosts from this study can be used for TSWV control.

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