Restricted Spread of *Tomato spotted wilt virus* in Thrips-Resistant Pepper

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ABSTRACT

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Spread of *Tomato spotted wilt virus* (TSWV) and population development of its vector *Frankliniella occidentalis* were studied on the pepper accessions CPRO-1 and Pikante Reuzen, which are resistant and susceptible to thrips, respectively. Viruliferous thrips were released on plants of each accession (nonchoice tests) or on plants in a 1:1 mixture of both accessions (choice tests) in small cages containing 8 or 16 plants. Significantly fewer CPRO-1 plants became infected in the primary infection phase in both tests. In the nonchoice test, virus infection of the resistant plants did not increase after the initial infection, but all plants eventually became infected when mixtures of both cultivars were challenged in the secondary infection phase. Secondary spread of TSWV from an infected resistant or susceptible source plant was significantly slower to resistant plants than to susceptible plants, independent of source plant phenotype. The restricted introduction and spread of TSWV in the thrips-resistant cultivar was confirmed in a large-scale greenhouse experiment. The restricted and delayed TSWV spread to plants of the resistant accession in both the cage and the greenhouse experiment was explained by impeded thrips population development. The results obtained indicate that thrips resistance may provide a significant protection to TSWV infection, even when the crop is fully susceptible to the virus.

Additional keywords: *Frankliniella occidentalis*, primary spread, secondary spread, vector resistance.

Tomato spotted wilt virus (TSWV), the type species of the genus *Tospovirus* within the family *Bunyaviridae*, is propagatively transmitted by thrips (Thysanoptera: Thripidae) and has a broad host range of over 1,000 plant species (10). Eight thrips species have been identified as vectors, of which *Frankliniella occidentalis* Pergande currently is considered to be the most important (13,37,39). The broad host range of this vector and its increasing resistance to insecticides (8,33,42) impede control of TSWV by insecticide application.

Current control strategies for TSWV include rogueing infected plants, the use of clean stock material (27), excluding thrips by greenhouse screens (34), air locks, or introducing natural enemies (16,25). As these control strategies are only partially successful, additional measures are needed to limit virus spread.

Host plant resistance to TSWV is available for a number of crops, including chrysanthemum (13), lettuce (11), pepper (3–5), and tomato (35). In addition, significant levels of resistance to thrips also have been reported in cabbage (36), chrysanthemum (7,21), groundnut (31), peanut (20), pepper (15,26), and tomato (23). Thrips resistance might affect the spread of TSWV either in a negative or positive way. Reduced spread of *Groundnut bud necrosis virus* (GBNV) was found in the groundnut accession Robut 33-1, which was attributed to fewer thrips on the plants of this accession than on thrips-susceptible accessions (1). In contrast, increased virus spread on a thrips-resistant cultivar has been reported for chrysanthemum (38). This outcome was explained by altered feeding behavior of *F. occidentalis* on the resistant chrysanthemum plants. Disturbed feeding behavior of *F. occidentalis* and *Thrips tabaci* also was reported on resistant cucumber and leek, respectively, resulting in fewer penetrations and reduced feeding time (18).

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Previous studies using pepper cultivars have revealed that resistance to thrips has little effect on the acquisition and inoculation of TSWV (26). In those studies, however, the impact of the thrips population development on the spread of the virus was not analyzed. Thrips reproduction was significantly lower on the thrips-resistant plants (26); therefore, it may reduce spread of TSWV in such cultivars.

In this study, the effects of thrips resistance on the spread of TSWV by *F. occidentalis* in pepper was analyzed, taking effects of thrips population development into account. To this end, both small-scale infection experiments as well as a large-scale greenhouse experiment were set up to validate the results.

MATERIALS AND METHODS

Thrips population, virus isolate, and pepper material used. The *F. occidentalis* population originated from a greenhouse infestation in lucerne (*Medicago sativa*). To produce viruliferous thrips, 0- to 4-h-old first instar larvae were confined to leaf disks (2.5 cm in diameter [i.d.]) from TSWV-infected *Datura stramonium* plants in a petri dish (3.4 cm i.d.) on 1.5% agar. After an acquisition access period (AAP) of 48 h, the larvae were transferred to virus-free leaf disks of *D. stramonium* until the adults emerged. The percentage of viruliferous adults was determined by testing 100 randomly sampled adults on Petunia leaf disks (40).

The TSWV isolate BR-01 (14) was maintained by thrips-mediated passages on *D. stramonium* plants. Extracts of these plants were mechanically inoculated on 2-week-old pepper seedlings, which served as the virus source in transmission studies 2 weeks post inoculation.

In all studies, the *Capsicum annuum* accessions "Pikante Reuzen" and "CPRO-1", susceptible and resistant, respectively, to *F. occidentalis* (26), were used. Both accessions, hereafter referred to as thrips susceptible (TS) and thrips resistant (TR), respectively, were verified to be equally susceptible to TSWV by me-

chanical inoculation (26). Resistance to thrips in the TR cv. CPRO-1 was defined previously by lack of reproduction, low preference, and minimal feeding damage (26).

Spread of TSWV to TR and TS plants in choice and nonchoice tests. Primary spread of TSWV (i.e., virus spread after introduction of viruliferous thrips) was studied by releasing 30 randomly selected adults that were allowed to acquire the virus as 0- to 4-h-old larvae, in the middle of thrips-proof cages (0.75 by 0.75 by 1 m) with 8 or 16 TR or TS plants (nonchoice tests). The 4-week-old plants (sixth-leaf stage) were placed in a square at a distance of ≈20 cm apart. In choice tests, 4 or 8 plants of each accession were placed together in cages, instead of using 8 or 16 plants of one accession. The choice and nonchoice tests each were performed three times. Development of TSWV symptoms and the number of larvae and adult thrips were scored on each plant at weekly intervals. The thrips were counted visually while turning and inspecting the leaves carefully to prevent dispersal of the adults. In addition, infection of test plants was monitored weekly by enzyme-linked immunosorbent assay (ELISA) using extracts of a leaf disk (1.3 cm i.d.) cut from a top leaf of each plant.

Spread of TSWV from an infected source plant to TS and TR plants. Secondary spread of TSWV (i.e., virus spread from infected to healthy plants) was studied after the release of nonviruliferous thrips to a TSWV-infected TR or TS plant surrounded by either 8 or 16 healthy plants of either accession. This resulted in four treatments with 8 plants and four treatments with 16 plants. Each treatment was replicated twice. Thirty nonviruliferous *F. occidentalis* adults were released at the base of the infected source plant in the middle of each cage. The number of thrips and the spread of the virus from the infected plant to the noninfected plants were scored at weekly intervals.

Greenhouse validation of thrips resistance on the spread of TSWV. Spread of TSWV and thrips population development in TR and TS pepper were analyzed in a greenhouse experiment in which these cultivars were exposed to the same thrips population. In total, 15 plots were arranged, each containing 25 plants. Five plots contained TS plants, five plots contained TR plants (nonchoice plots), and five plots contained a 1:1 mixture of TR and TS plants (choice plots). Plants were grown in 5-liter plastic pots at a 45-cm distance within a row and at a 50-cm distance between rows. The 15 plots were surrounded by "edge-plots" to prevent environmental influences affecting the outer plots. Treatments were randomly assigned to the plots. Forty randomly selected adults, that were allowed to acquire TSWV as 0- to 4-h-old larvae on infected leaf disks, were released at five points in each plot when the plants were 4 weeks old. The experiment was conducted from February to April in Wageningen (the Netherlands), during which the temperature ranged from 23 to 31°C during the day and was maintained at 20°C during the night. Plants were watered daily with 200 ml of water using a dripping system, and grown under a 16-h light and 8-h dark cycle.

Infected plants and the number of thrips were scored at weekly intervals. Infection of plants was confirmed by ELISA. At the end of the experiment, thrips were collected from each plot and tested for their ability to transmit TSWV in a Petunia leaf disk assay (40) to determine the percentage of viruliferous thrips per plot.

Virus detection by ELISA. TSWV infection was monitored weekly by analysis of 1.3-cm-i.d. leaf disks by double-antibody sandwich ELISA (12,30). Each disk was ground in 150 µl of phosphate-buffered saline, containing 0.05% Tween 20, pH 7.2. Polyclonal antibodies, raised in rabbits, against the TSWV nucleocapsid protein were used at a concentration of 1 µg/ml.

Statistical analysis. The percentage of virus-infected plants obtained at each weekly interval in the different experiments was analyzed as binomial distributed variables with GENSTAT (29) and compared for each treatment. The number of thrips found on TS and TR plants was analyzed by Kruskal-Wallis one-way analysis of variance.

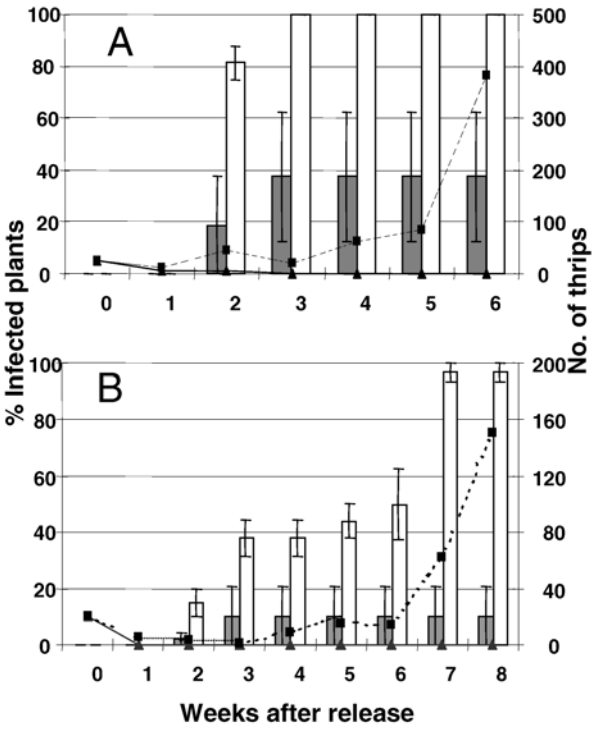

Fig. 1. Development of *Tomato spotted wilt virus* infection in **A,** 8 or **B,** 16 thrips-susceptible (TS; white bars) or thrips-resistant (TR; dark bars) pepper plants in nonchoice tests after release of viruliferous thrips. Error bars indicate the standard errors of the mean. Lines depict the average number of *Frankliniella occidentalis* on TS (dashed line) or TR (solid line) plants.

RESULTS

Spread of TSWV to TR and TS plants in nonchoice tests. In the nonchoice tests, plants of the TR and TS cultivars were separately exposed to adult thrips, of which an average of 27% were viruliferous (data not shown). The first virus-infected plants were observed 2 weeks after release of thrips in these tests (Fig. 1). Plants of the TS accession became readily infected in both independent replications but the number of infected TR plants remained significantly ($P < 0.05$) lower and did not increase after 3 weeks following thrips release (Fig. 1). On the TS plants, thrips numbers started to increase 3 weeks after release, whereas no thrips could be discerned on the TR plants 3 weeks following release. The difference in thrips numbers between the accessions became significant ($P < 0.05$) from the third week onward (Fig. 1).

Spread of TSWV to TR and TS plants in choice tests. In the choice tests, in which released thrips had access to equal numbers of TS and TR plants, the first infected plants were found 2 to 3 weeks after thrips release (Fig. 2). Although eventually all plants became infected in this test, virus spread to the TR plants was significantly delayed compared with the TS plants. Thrips numbers increased 3 weeks after release and were not significantly ($P > 0.05$) lower on the resistant plants, indicating that thrips reproduction on TS plants resulted in similar vector pressure on both accessions.

Spread of TSWV from an infected source plant to TS and TR plants. Secondary spread of TSWV was assessed by releasing nonviruliferous adult thrips on an infected TS or TR source plant in cages together with noninfected plants of the TR or TS accession. In two independent experiments (using either 8 or 16 plants), the first infections were observed ≈4 weeks after releasing the thrips (Figs. 3 and 4). After these initial infections, the number of TR plants becoming infected increased at a significantly lower rate ($P < 0.05$) than the number of infected TS plants in the four

different combinations of infected source and healthy test plants (Figs. 3 and 4). The rapid infection of TS plants occurred independently whether a TS or TR plant was used as virus source (Figs. 3 and 4). Compared with TS, the infection of TR plants was considerably delayed when 8 plants were exposed (Figs. 3A and 4A) and slightly lower when 16 plants were exposed to the virus sources used (Figs. 3B and 4B). This effect might be due to a lack of thrips population development on TR plants. Indeed, significantly ($P < 0.05$) fewer thrips were consistently found on TR plants than on TS plants ≈4 weeks after release. This trend was independent of virus source and number of plants per treatment (Figs. 3 and 4).

Greenhouse validation of thrips resistance on the spread of TSWV. The small-scale experiments described above indicate that a substantial level of thrips resistance may improve control of TSWV in pepper. To validate these results, performance of TR pepper was evaluated in a large-scale greenhouse experiment. Thrips were released at five points in each nonchoice or choice plot. Of the released adults, 53% transmitted TSWV in a Petunia leaf disk assay (data not shown); hence, ≈21 of the 40 released adults in each plot were viruliferous. The first systemically infected TR and TS plants were observed 2 weeks after thrips release in both the nonchoice and choice plots (Fig. 5). The number of initial infections in TR plots was considerably lower during the first 2 weeks and secondary spread was significantly delayed compared with TS plots ($P < 0.05$). However, at 12 weeks after thrips release, 97% of the TR plants and all TS plants became infected. The delayed spread of the virus in the TR plots also was reflected in the percentage of viruliferous thrips sampled at the end of the experiment, being 14% (TR plots) compared with 25% (TS plots).

Thrips numbers were significantly lower on TR plants than on TS plants during the entire experiment in the choice and non-

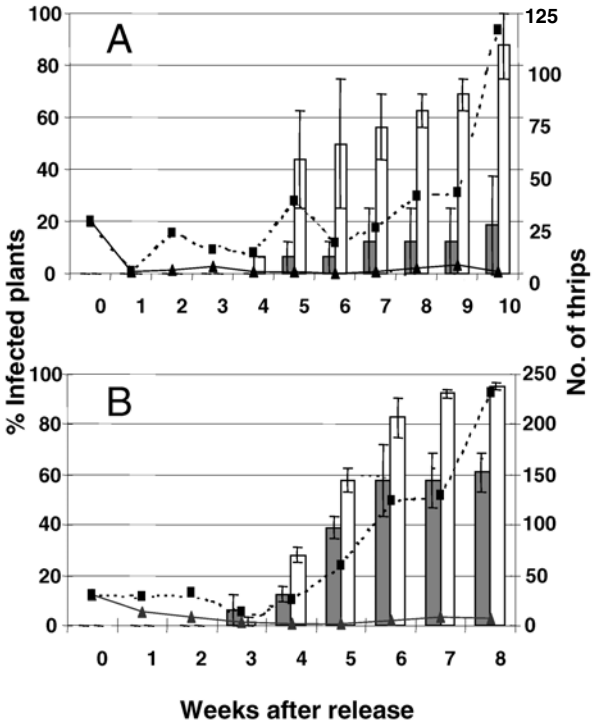

Fig. 3. Spread of *Tomato spotted wilt virus* from an infected thrips-resistant (TR) plant after the release of nonviruliferous *Frankliniella occidentalis* to **A,** 8 or **B,** 16 thrips-susceptible (TS; white bars) or TR (dark bars) pepper plants. Error bars indicate the standard errors of the mean. Lines depict the average number of *F. occidentalis* on TS (dashed line) or TR (solid line) plants.

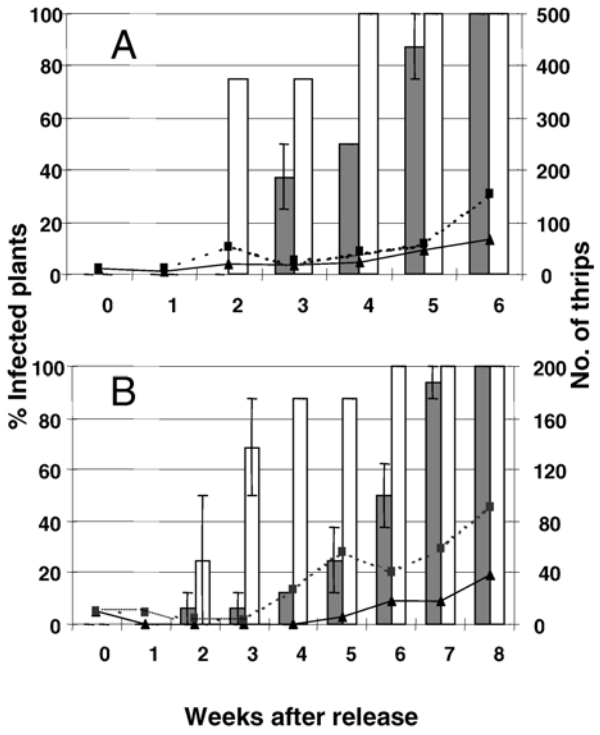

Fig. 2. Development of *Tomato spotted wilt virus* infection in **A,** 8 or **B,** 16 pepper plants in choice tests after the release of viruliferous thrips. Half of the plants were thrips-susceptible (TS; white bars) and half were thrips-resistant (TR; dark bars). Error bars indicate the standard errors of the mean. Lines depict the average number of *Frankliniella occidentalis* on TS (dashed line) or TR (solid line) plants.

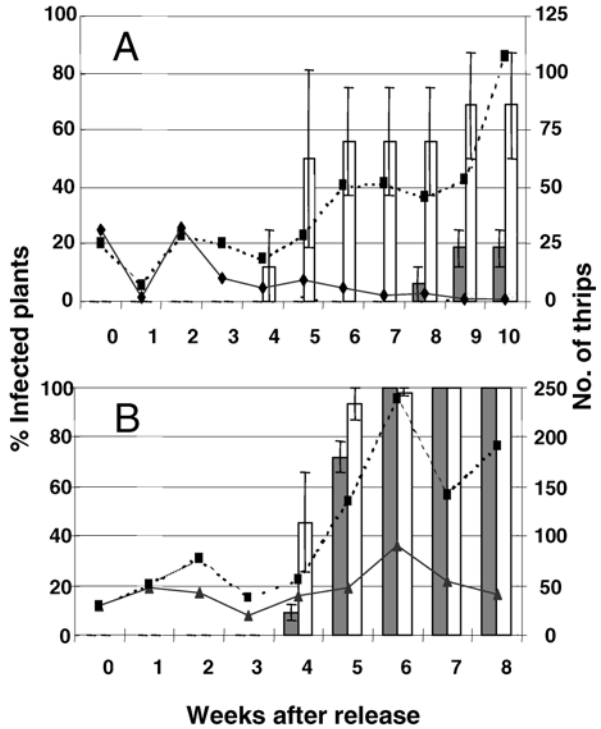

Fig. 4. Spread of *Tomato spotted wilt virus* from an infected thrips-susceptible (TS) plant after the release of nonviruliferous *Frankliniella occidentalis* to **A,** 8 or **B,** 16 TS (white bars) or thrips-resistant (TR; dark bars) pepper plants. Error bars indicate the standard errors of the mean. Lines depict the average number of *F. occidentalis* on TS (dashed line) or TR (solid line) plants.

choice plots ($P < 0.05$) (Fig. 5). Few thrips could be discerned on TR plants during the first 6 weeks after release, whereas high numbers were found on the TS plants in this period. The increased thrips numbers on TR plants after 6 weeks might have been due the flowering of the plants and, hence, the availability of pollen, an essential food source for this thrips species.

DISCUSSION

The effect of thrips resistance on spread of TSWV was assessed on TR and TS pepper accessions in both choice and nonchoice tests. In choice tests, released viruliferous thrips had access to plants of both accessions; whereas, in nonchoice tests, access was limited to plants of one accession. Infections occurring during the first 2 weeks were considered primary infections, resulting from inoculations by introduced viruliferous thrips, whereas later, secondary, infections were considered the result of inoculations by offspring (Figs. 1 and 2). In the small-scale studies, using 8 or 16 plants per accession, the primary infection rate was significantly lower for TR plants. Apparently, released thrips failed to reproduce on TR plants; therefore, no secondary spread occurred on these plants in the nonchoice cage tests. In contrast, the number of infected TS plants increased during the third and fourth week (Figs. 1A and B) due to successful vector reproduction.

In the choice tests, the number of primarily infected TR plants remained significantly lower than for TS plants (Fig. 2). The difference was larger than expected, because the inoculation rate was somewhat lower on TR than on TS leaf disks after inoculation access periods longer than 16 h (26). This difference might be caused by factors playing a role in the transmission on plants but not on leaf disks. These factors may be related either to a different (feeding) behavior of thrips on TR plants, a more active dispersal of thrips to TS plants, or a higher preference for these plants. A different feeding behavior of *F. occidentalis* and *T. tabaci* has been reported for TR cucumber and leek, respectively (18), but this effect on TSWV transmission was not analyzed in these studies.

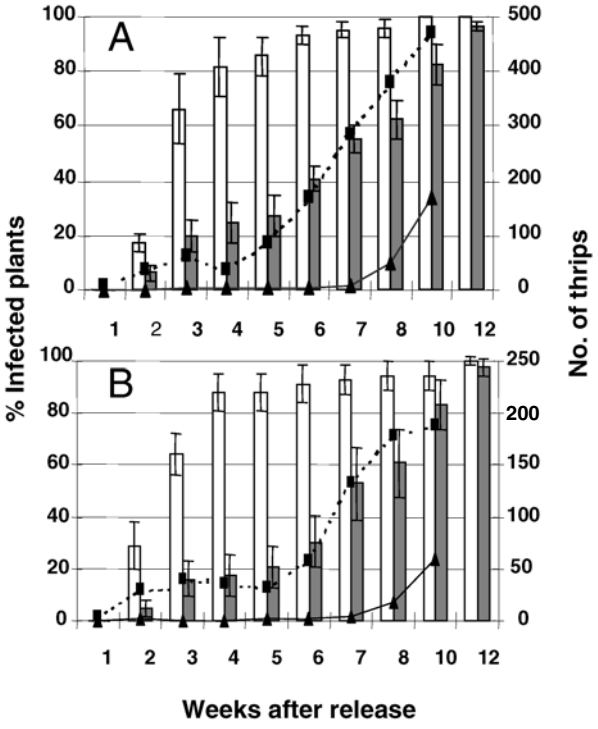

Fig. 5. Development of *Tomato spotted wilt virus* infection in a thrips-resistant (TR; dark bars) or thrips-susceptible (TS; white bars) accession in greenhouse plots with **A,** plants of one accession or **B,** in plots with a 1:1 mixture of TR and TS plants of both accessions after the release of viruliferous *Frankliniella occidentalis*. Error bars indicate the standard errors of the mean. Lines depict the average number of *F. occidentalis* on TS (dashed line) or TR (solid line) plants.

In the choice tests, the rate of virus transmission to TR plants clearly differed from that in the nonchoice tests. Spread in TR plants followed the same trend as for TS plants, but with a delay of 2 to 4 weeks (Figs. 2A and B). On TR plants, thrips did not reproduce in the nonchoice tests; hence, secondary spread to TR plants in the choice test was attributed to thrips that originated from the TS plants.

Secondary virus spread of TSWV was studied in choice tests by releasing nonviruliferous thrips in cages with an infected source plant and healthy plants. In two replicate experiments using either a cohort of 8 or 16 healthy plants, the rate of secondary spread of TSWV was significantly delayed among TR plants compared with TS plants.

Differences in virus spread to TR and TS plants were much smaller and reached higher levels when the virus was acquired from a TS source than from an infected TR source. Apparently, the efficient reproduction and development of the thrips on the TS source plant resulted in a more efficient virus spread. This indicates that infected TS plants support virus epidemics more efficiently than infected TR plants. Although TSWV often is spread in a greenhouse or field by primary infections (9,17,24,41), our results illustrate that the significance of secondary infections in TS crops should not be ignored.

The effect of thrips resistance on both virus spread and thrips population development, observed in small-scale experiments, was confirmed in a greenhouse experiment. Plots with plants of both pepper accessions were exposed to the same initial infection pressure. The rate at which TR plants became infected was significantly lower in both choice and nonchoice plots, consistent with the results from small-scale experiments. On TR plants, fewer primary infections were produced by released viruliferous thrips and secondary spread was delayed. Thrips failed to reproduce on TR plants; therefore, the increase of infected TR plants is the result of secondary spread by thrips dispersing from TS plots. The inoculation efficiency of TSWV on TR and TS plants is similar (26); therefore, the delayed secondary spread of TSWV to TR plants compared with TS plants may be due to slower dispersal of adults from TS to TR plants. An alternative explanation might be that adults prefer virus-infected TS plants over non-infected TR plants and, therefore, do not readily move from the infected plants in TS plots. The finding that a significantly higher percentage of viruliferous thrips were caught in the TS plots supports limited dispersal between the plots.

The impeded virus spread due to thrips resistance of the host plant can be correlated to both restricted reproduction and low host preference, because fewer thrips are found on TR than on TS plants in the nonchoice as well as choice plots (Fig. 5A and B). Restriction of virus spread on thrips-resistant accessions also has been found in other investigations using different virus–thrips–host systems. The lower incidence of GBNV on thrips-resistant groundnut (cv. Robut 33-1) was attributed to a lower thrips density compared with the more susceptible cv. TMV 2 (1). Some *Lycopersicon esculentum* Mill. accessions were less susceptible to TSWV in thrips inoculation experiments than others, although all accessions were highly susceptible to mechanical inoculation of the virus (22). Vector resistance also reduced virus incidence in studies with *Grapevine fanleaf virus*, *Potato leafroll virus*, *Rice ragged stunt virus*, and *Tomato yellow leaf curl virus*, which are transmitted by nematodes, aphids, planthoppers, or whiteflies, respectively (2,6,28,32). The precise mechanism by which transmission is restricted remains unknown (19). Our previous work on the TR pepper accession revealed that thrips resistance does not necessarily lead to lower virus acquisition or inoculation frequency (26). Apparently, the seemingly indirect effects

of thrips resistance on vector pressure result in significant restriction of virus spread even in a host that is fully susceptible to the virus.

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