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Effects of imidacloprid on transmission of tomato spotted wilt tospovirus to pepper, tomato and tobacco by *Frankliniella fusca* Hinds (Thysanoptera: Thripidae)

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Abstract

Rates of transmission of tomato spotted wilt tospovirus (TSWV) by tobacco thrips, *Frankliniella fusca* Hinds, to imidacloprid-treated and untreated tomato, pepper and tobacco were measured in greenhouse and small-plot field trials. The incidence of TSWV was reduced in greenhouse assays with all 3 crops receiving a soil application of imidacloprid at a rate of 9.9 g [AI]/1000 plants. Levels of TSWV were also reduced in small-plot field trials of tomato and pepper plants receiving transplant applications of imidacloprid at the same rate. No *F. fusca* were recovered from imidacloprid-treated tobacco (9.9 g [AI]/1000 plants) 24 days following an initial infestation. In the greenhouse, *F. fusca* populations reached higher levels on healthy than TSWV-infected tobacco. Applications of soil-applied imidacloprid reduced the number and duration of probing/feeding bouts by *F. fusca* on pepper and mustard (*Brassica rapa* L.). Reduced probing and feeding by viruliferous thrips on imidacloprid-treated plants may contribute to less TSWV incidence as observed in the field and greenhouse experiments.

Keywords: *Frankliniella fusca*; Imidacloprid; Tomato spotted wilt tospovirus

1. Introduction

Tomato spotted wilt tospovirus (TSWV) has become common in both ornamental and row crop production and is capable of causing severe losses in a number of susceptible crops (Ullman et al., 1997). TSWV has caused extensive crop losses in Florida, Georgia, Louisiana, Texas and North Carolina (Puche et al., 1995; Johnson et al., 1995; Goodenough et al., 1985; Mitchell and Smith, 1991; Cho et al., 1995). Management has proven to be difficult because both the virus and its thrips vectors have extremely broad host ranges. Further, because current approaches to TSWV management are costly and of limited effectiveness, their routine use cannot be justified (Lewis, 1997).

TSWV is persistently transmitted by adults of at least eight species of thrips that have acquired the virus by feeding as a first instar on an infected host plant (Mound, 1996). In North Carolina, the tobacco thrips, *Frankliniella fusca* Hinds, is considered to be the most important TSWV vector (Cho et al., 1995). Patterns of TSWV movement suggest that secondary spread is limited and most infections result from primary spread (Camann et al., 1995; Latham and Jones, 1997; Wilson, 1998). The predominance of primary spread helps to explain why controlling vector populations within a crop has had minimal effects on lowering the final incidence of infection (Funderburk et al., 1990; McPherson et al., 1992; Todd et al., 1996). Most insecticides do not intoxicate thrips quickly enough to prevent transmission of TSWV, which can be transmitted to a healthy plant by an infectious thrips in as little as 5–10 min (Wijkamp and Peters, 1993).

The chloronicotinyl insecticide imidacloprid (Bayer Corp., Kansas City, MO) is highly effective against many sucking insects including thrips (Elbert et al., 1990). Preplant applications of imidacloprid in potato have reduced the incidence of potato leafroll virus (PLRV) in field studies (Boiteau and Singh, 1999; Woodford and Mann, 1992). Imidacloprid applied to the soil at the time of planting reduced the incidence of barley yellow dwarf virus (BYDV) in oats and wheat (Gourmet et al., 1996)

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and maize (Abraham and Epperlein, 1999). In laboratory studies, applications of neonicotinoid compounds have provided moderate reductions in the incidence of potato Y potyvirus (PVY) in pepper (Collar et al., 1997) and potato (Harrewijn et al., 1998) and of sugarcane mosaic potyvirus (SMV) in sorghum (Harvey et al., 1996).

Herein, we report on the effects of preplant applications of the Admire® 2F formulation of imidacloprid on transmission of TSWV by tobacco thrips, *Frankliniella fusca* Hinds, to tomato, pepper, and tobacco in the greenhouse and to tomato and pepper in the field. In addition, we report on the probing and feeding activity of *F. fusca* on imidacloprid-treated pepper and mustard (*Brassica rapa* L.) plants, as measured by electronic penetration graphs (EPG).

2. Materials and methods

2.1. Thrips and virus culture

Frankliniella fusca were obtained from an imidacloprid-susceptible colony maintained on green bean pods (*Phaseolus vulgaris* L.) in an enclosed laboratory chamber held at 24°C, 65% RH and a photoperiod of 14 : 10 (L : D) h. Viruliferous, adult *F. fusca* were obtained by releasing first instar thrips (0–12 h old) onto excised, TSWV-infected *Emilia sonchifolia* (L.) DC. ex Wight foliage. After a 48 h acquisition access period, thrips were transferred to an uninfected bean pod and reared to adult in 474 ml clear, plastic cups (Sweetheart Cup Co., Inc. Chicago, IL) with fine-mesh screened lids (Bedbug 110; Greenthumb Group, Downer's Grove, IL). Approximately 24 h following eclosion, adults were aspirated into 2.5 ml disposable Pasteur® pipettes (10 thrips/pipette) and the ends of the pipettes sealed with Parafilm® to prevent escape. Aspirated thrips were then released onto susceptible plants after a 2 h starvation period. In all experiments, 10 potentially viruliferous adults were released onto each individually caged plant.

Three isolates of TSWV were used in these experiments. A tobacco isolate (TSWV-RG2), used for greenhouse transmissions to tobacco, was obtained in 1995 from an infected tobacco plant in Carteret County. A tomato isolate (TSWV-GT), used for greenhouse and field transmissions to tomato, was collected in 1996 from an infected tomato plant in Clarke County, GA. A pepper isolate (TSWV-P), used for transmissions to pepper, was collected in 1995 from an infected pepper plant in Wayne, County, NC. Each isolate was maintained in *E. sonchifolia* plants held in insect-proof containers in a greenhouse at temperatures of 28 : 20°C (L : D) and a photoperiod of 14 : 10 (L : D) h. Cylindrical, insect-proof containers (15 cm dia. × 30 cm ht) were constructed of 5 mm, clear Vivak plastic (AIN Plastics Corp, Greensboro, NC) covered with Bed Bug 110 fine-mesh screening. TSWV isolates were transferred to fresh *E. sonchifolia* plants every 12 weeks using *F. fusca* as vectors. Newly expanded, symptomatic *E. sonchifolia* foliage was used as the virus acquisition source in all assays. TSWV infections were serologically confirmed by double antibody sandwich, enzyme-linked immunosorbent assay (DAS-ELISA) using commercial test kits (Agdia Inc., Elkhart IN). Following incubation, optical densities (OD) at 405 nm were read using a THERMOmax microtiter plate reader (Molecular Devices Corp., Menlo Park, CA). Plants were scored as infected if the OD exceeded the mean plus 3 standard deviations of the non-infected controls of the same plant species and a visible color change was evident within test wells.

2.2. Greenhouse transmission assays

Tobacco (*N. tabacum* var. 'K326'), tomato (*L. esculentum* var. 'Mountain Pride') and pepper (*C. annuum* var. 'Jupiter') seeds were germinated in black plastic transplant trays under insect-proof cages in a virus-free greenhouse. At the first true leaf stage, 120 plants of each species were transplanted individually into black, plastic pots (15 cm dia. × 20 cm ht) and covered with insect-proof cages.

In separate greenhouse experiments examining rates of transmission to imidacloprid-treated and untreated plants, experimental blocks of pepper, tomato, and tobacco were arranged in a randomized complete block design and replicated 3 times with 40 plants per replication (total of 120 plants per species). Sixty plants of each species, in the 2–4 leaf stage, were treated with a soil application of imidacloprid at the rate of 9.9 g [AI]/1000 plants. Imidacloprid was delivered to each plant in a 150 ml aqueous suspension poured directly onto the soil at the base of each plant. The remaining 60 plants of each species served as an untreated control and received a 150 ml aliquot of water at the time of insecticide application. All plants were caged immediately following insecticide treatment. Six days later, 10 potentially viruliferous adult *F. fusca* were released onto each caged plant where they remained for 48 h. Cages were then removed and plants were treated with a foliar application of imidacloprid at 7.1 g [AI]/1000 plants to kill released adult thrips and progeny. All plants were again caged. Twenty-one days later, 4 randomly selected foliage samples, each approximately 1 cm^2, were removed from each plant, labeled, and stored at -80°C until a serological assay was conducted.

An additional greenhouse experiment was conducted to measure the effect of imidacloprid and TSWV infection on population growth of *F. fusca* on tobacco (var. K326). Experimental treatments included 2 levels of imidacloprid (9.9 g [AI]/1000 or untreated) and 2 levels of infection with the TSWV-RG2 isolate (infected or

non-infected) arranged in a 2×2 factorial design. Each treatment combination was replicated 3 times in a randomized complete block design with 20 plants per treatment combination. Tobacco was mechanically inoculated from TSWV-infected *Nicotiana benthamiana* Domin (TSWV-RG2) 14 days prior to release of *F. fusca*. Mechanical sap inoculations were conducted by mixing TSWV-infected *N. benthamiana* sap extract 1 : 10 in inoculation buffer containing 0.01 M Tris buffer (pH 7.8), 5.7 mM cysteine hydrochloride and 1 mM sodium sulfite. The inoculation preparation was held in an ice bath during mechanical inoculations. On the same day of inoculation, imidacloprid was applied over the soil surface at the base of plants, as described previously. Six days later, 10 non-viruliferous, adult *F. fusca* from the laboratory colony were released onto individually caged tobacco plants in all 4 treatments. Twenty-four days following release, all *F. fusca* lifestages were recovered from each plant by cutting plants at the soil surface and placing them individually in insect-proof containers inside a desiccation chamber set at 28°C and 20% RH. One fresh bean pod was added to each container. As the thrips left the desiccating tobacco plant, they concentrated on the bean pod, which remained succulent. Pods were removed from the containers within 3 days after tobacco plants had fully desiccated and all adult and immature *F. fusca* present on the bean pods were collected and counted. Immature thrips collected from the TSWV-infected treatments were allowed to develop to the adult stage and individually subjected to a petunia leaf disk assay (Wijkamp and Peters, 1993). Circular leaf discs (1 cm^2) of *Petunia hybrida* var 'Celebrity Blue' were used in the assay to document transmission of TSWV by individual thrips. Lesions forming on petunia discs were confirmed as TSWV infections using DAS-ELISA (Agdia Inc., Elkhart IN).

2.3. Field transmission assays

A small-plot field experiment was conducted to assess transmission rates of TSWV to imidacloprid treated and untreated tomato (*L. esculentum* var. Mountain Pride) and pepper (*C. annuum* var. Jupiter). Virus-free plants 10–15 cm tall, were transplanted into small plots arranged in a randomized complete block design, replicated 3 times with 40 plants per replication (total of 120 plants/species). Separate experiments were conducted for tomato and pepper. Tomatoes were planted 45 cm apart within rows that were on 152 cm centers and peppers were planted 38 cm apart within rows that were on 96 cm centers. In each replicate, half of the plants were treated with imidacloprid (11.3 g [AI]/1000 plants) applied in transplant water (150 ml per plant), while only water was applied to the remaining half. Immediately following transplant, all plants were caged in insect-proof cages to allow the imidacloprid to become systemic. Eight days later, 10 potentially viruliferous adult *F. fusca* were released onto each caged plant where they remained for 48 h. Plants were then treated with a foliar application of imidacloprid at 7.1 g [AI]/1000 plants. Twenty-one days later, foliage samples were collected from all plants and subjected to DAS-ELISA to detect TSWV.

2.4. Electronic penetration graphs

Plant penetration associated with probing and feeding by adult female *F. fusca* on imidacloprid treated and non-treated plants was compared with electronic penetration graphs (EPG) obtained using a direct current (DC) system (Tjallingii, 1988). The EPG system, (IFM II, Oklahoma Engineering and Technical Services, Oklahoma City, OK) was connected to a strip chart recorder. All feeding assays were conducted at 22°C and 50% RH. After fasting for 1 h, adult female *F. fusca* were attached at the dorsal surface of the pronotum to a 50 μm gold wire (Premion®, Alfa Aesar Inc.) using a small droplet of general purpose silver conductive paint (Alfa Aesar, Inc.). To immobilize thrips while the wire was being attached, they were placed individually on a screen-covered vacuum-table and, if necessary, exposed to small quantities of CO_2. Wired thrips were placed on the abaxial surface of a fully expanded leaf in the upper canopy of the test plant and the other end of the gold wire connected to the EPG system. Thrips were given 30 min to acclimate to their surroundings before data were recorded. Probing and feeding activity of each thrips was recorded for 1 h (amplifier input resistance of $10^8\ \Omega$ and a chart recorder band width of 50 Hz) with a recorder chart speed of 1 cm/min. From each 60 cm chart record, the total number of probing events, or potential drops was recorded, as was the duration of each potential drop.

Electronic penetration graphs were recorded for *F. fusca* adult females on untreated and on imidacloprid treated mustard, *Brassica rapa* L., and pepper (var. 'Jupiter') plants. Dense pubescence on the abaxial leaf surfaces of both tomato and tobacco impeded movement of wired insects on leaf surfaces. Mustard, with glabrous leaf surfaces that did not inhibit thrips movement, was used in place of either species. All plants were germinated and grown under insect-proof cages in a virus-free greenhouse and transplanted individually into 15 cm pots at the fourth leaf stage. At this stage, 2 imidacloprid treatments were applied (7.1 and 14.2 g [AI]/1000 plants) to sets of 5 plants for each rate. Five additional plants of each species were left untreated and served as controls. Plants remained caged for 6 days to allow for systemic translocation of imidacloprid. Additional plants were treated (or left untreated) weekly and rotated into the experiments so that plant age remained constant throughout the experiment.

Because the EPG system could monitor only 3 thrips simultaneously, each one hour monitoring session included one plant treated with one rate of imidacloprid, one untreated plant and one blank in which voltage from the feeding monitor was supplied to a pot containing only potting soil and an untreated plant. The latter was included to detect random potential drops on the chart output caused by background interference. Due to this constraint, only 5 sets of 3 EPGs could be completed each day. Consequently, separate experiments were conducted for each plant species and each rate of imidacloprid. Each experiment paired thrips on imidacloprid-treated (one rate) plants with thrips on untreated plants of the same species. In the experiments including *B. rapa,* a total of 50 and 15 sets (set includes a recording on imidacloprid treated plant, untreated plant and blank) of records were obtained for imidacloprid at 7.1 and 14.2 g [AI]/1000 plants, respectively. In experiments with pepper, a total of 50 and 30 sets of records were obtained at the 2 imidacloprid rates, 7.1 and 14.2 g [AI]/1000, respectively.

2.5. Statistical analysis

All statistical tests were conducted with SAS, ver. 7 (SAS Institute, 1998). Data from both field and laboratory transmission assays were square root transformed, whereas count data obtained from thrips recovered from insecticide treated and untreated plants and parameters measured from the EPG charts were log transformed for normalization of variance. Data from each experiment were subjected to ANOVA (PROC GLM) and treatment means in greenhouse and laboratory transmission experiments and parameter means obtained from the EPG experiments were compared using *F*-tests ($\alpha = 0.05$).

3. Results

3.1. Greenhouse and field experiments

Imidacloprid applied as a soil treatment reduced the final incidence of TSWV in pepper ($P = 0.0052$), tomato ($P = 0.0103$), and tobacco ($P = 0.0032$) in the greenhouse experiment (Table 1). Similar results were obtained in the field experiments, although the proportion of infected plants in the untreated controls tended to be lower than in the greenhouse experiment (Table 1). Imidacloprid applied at transplant reduced TSWV infections in both pepper ($P = 0.0424$) and tomato ($P = 0.0007$) compared to untreated control plants. The reductions in TSWV incidence were similar to those observed in the greenhouse experiment (74% greenhouse vs. 73% field for pepper and 82% greenhouse vs. 87% field for tomato).

In the separate experiment examining thrips development, no *F. fusca* were recovered from the imidacloprid-treated plants 24 days after adults were released, whereas an average of 3.3 thrips/plant were recovered from the untreated plants. In the absence of imidacloprid, fewer total *F. fusca* were recovered after 24 days on TSWV-infected (0.9 thrips/plant) than on uninfected tobacco (5.6 thrips/plant). This pattern held for both adult (infected = 0.4; uninfected = 2.8) and immature thrips (infected = 0.5; uninfected = 2.8). Only 6.4% (2 of 22) of the thrips collected as immatures from infected tobacco transmitted TSWV in the petunia leaf disk assay.

3.2. Electronic penetration graphs

Based on electronic penetration graphs, adult female *F. fusca* probed less frequently and the probes were of shorter duration on imidacloprid-treated than on untreated mustard (Table 2) and pepper (Table 3) plants.

Table 1
Mean (± SEM) percent transmission of TSWV by *Frankliniella fusca* to imidacloprid-treated and healthy pepper, tomato and tobacco[a]

Experiment	Pepper[c]		Tomato[d]		Tobacco[e]	
	UTC	Imidacloprid	UTC	Imidacloprid	UTC	Imidacloprid
Greenhouse[b]	41.3 ± 0.06a ($N = 75$)	9.3 ± 0.04b ($N = 75$)	80.0 ± 0.05a ($N = 75$)	14.7 ± 0.04b ($N = 75$)	82.5 ± 0.05a ($N = 63$)	11.1 ± 0.04b ($N = 63$)
Field[b]	32.1 ± 0.06a ($N = 53$)	8.8 ± 0.04b ($N = 57$)	64.3 ± 0.07a ($N = 56$)	8.3 ± 0.04b ($N = 60$)	N/A	N/A

[a]Means ± SEM reported from data analyzed by general linear models (GLM) procedure. Means separation ($\alpha = 0.05$) between imidacloprid-treated and non-treated based on *F*-test.

[b]Imidacloprid applied at 9.9 g [AI]/1000 plants in greenhouse assay and 11.3 g [AI]/1000 plants in field assay.

[c]Pepper plants scored TSWV-infected had optical densities ranging from 3.791 to 4.119 whereas, uninfected plants ranged from 0.074 to 0.106 in greenhouse experiments and from 1.354 to 3.011 and 0.098 to 0.109, respectively, in field experiments.

[d]Tomato plants scored TSWV-infected had optical densities ranging from 3.494 to 4.156 whereas uninfected plants ranged from 0.069 to 0.099 in greenhouse experiments and from 1.595 to 3.556 and 0.094 to 0.112, respectively, in field experiments.

[e]Tobacco plants scored TSWV-infected had optical densities ranging from 2.614 to 3.939 whereas uninfected plants ranged from 0.064 to 0.078 in greenhouse experiments.

Table 2
Mean (± SEM) number and duration of probing/feeding bouts by *Frankliniella fusca* on imidacloprid-treated and non-treated mustard plants[a]

Imidacloprid treatment	Mean number of potential drops/h[b]	Mean duration (min) of potential drops[b]
7.1 g [AI]/1000 plants		
UTC (thrips)	2.12 ± 0.07a	1.41 ± 0.09a
Treatment (1.0 fl oz)	0.70 ± 0.11b	1.28 ± 0.15b
14.2 g [AI]/1000 plants		
UTC (thrips)	1.53 ± 0.04a	0.79 ± 0.05a
Treatment (2.0 fl oz)	0.20 ± 0.09a	0.06 ± 0.03a

[a]Mean number of random potential drops/h in the thrips-free control was 0.04 in each experiment.
[b]Means reported from back-transformed data analyzed by general linear models (GLM) procedure.
Different rates of imidacloprid represent separate experiments. Means within columns for a given experiment not followed by the same letter are significantly different ($\alpha = 0.05$) by *F*-test.

Table 3
Mean (± SEM) number and duration of probing/feeding bouts by *Frankliniella fusca* on imidacloprid-treated and non-treated pepper plants[a]

Imidacloprid treatment	Mean number of potential drops/h[b]	Mean duration (min) of potential drops[b]
7.1 g [AI]//1000		
UTC (thrips)	1.53 ± 0.08a	0.39 ± 0.04a
Treatment (1.0 floz)	0.03 ± 0.01b	0.01 ± 0.01b
14.2 g [AI]//1,000		
UTC (thrips)	1.84 ± 0.09a	0.52 ± 0.11a
Treatment (2.0 fl oz)	0.28 ± 0.03b	0.04 ± 0.02b

[a]Means reported from back-transformed data analyzed by general linear models (GLM) procedure. Different rates of imidacloprid represent separate experiments. Means within columns for a given experiment not followed by the same letter are significantly different ($\alpha = 0.05$) by *F*-test.
[b]Mean number of random potential drops/h in the thrips-free control was 0.02 in each experiment.

On mustard treated with imidacloprid at the lower rate, potential drops were fewer ($P = 0.0024$) and of shorter duration ($P = 0.0156$) than on non-treated control plants. Similar results were observed on mustard treated with the high rate of imidacloprid, although the number ($P = 0.2725$) and duration ($P = 0.1217$) of potential drops did not differ significantly from non-treated plants. The lack of statistical significance at the higher rate is probably due to limited replication ($n = 15$). On pepper, potential drops at both the 7.1 and 14.2 g rates of imidacloprid were fewer ($P < 0.0001$ and 0.0003, respectively) and of shorter duration ($P = 0.0014$ and 0.0008, respectively) than on non-treated plants. On both pepper and mustard, background interference was minimal, as indicated by the occurrence of very few random potential drops in the untreated control (0.04 for the mustard experiments and 0.02 for pepper experiments).

4. Discussion

Attempts to reduce the incidence of TSWV by controlling thrips with insecticides have produced conflicting results. Todd et al. (1996) reported that in small plot experiments the final incidence of TSWV in peanut was reduced following applications of either acephate or a combination of phorate plus acephate. However, in a large-plot experiment, neither aldicarb nor acephate alone or in combination reduced the final incidence of TSWV. McPherson et al. (1992) reported that transplant applications of either aldicarb or carbofuran followed by weekly applications of acephate reduced the final incidence of TSWV in flue-cured tobacco, whereas transplant applications without subsequent foliar applications of acephate, had little effect on the incidence of TSWV. In a subsequent study, McPherson et al. (1998) reported that foliar applications of imidacloprid at 1, 3, and 6 weeks post-transplant did not reduce the incidence of TSWV in flue-cured tobacco. In contrast, transplant applications of imidacloprid alone and in combination with acibenzolar-S-methyl (Novartis, Greensboro, NC) reduced the final incidence of TSWV in tobacco in large-scale field trials in Georgia by 30–50% (Pappu et al., 2000).

In our greenhouse and field experiments, applications of imidacloprid to the soil dramatically reduced transmission of TSWV by *F. fusca* to pepper, tomato, and tobacco (Table 1). Not surprisingly, no thrips were recovered from imidacloprid-treated tobacco in the greenhouse experiment in which adult *F. fusca* were released on the plants only 6 days after imidacloprid was applied. Imidacloprid applied at transplanting has been reported to control both thrips and aphids on tobacco for at least 14 days (Crow et al., 1996; McPherson et al., 1998). On other crops, residual activity against aphids has been reported to persist at least 28 days (Harvey et al., 1996; Gourmet et al., 1996; Woodford and Mann, 1992).

In the absence of imidacloprid, we recovered significantly fewer *F. fusca* from TSWV-infected than from uninfected tobacco plants. Similar results were obtained with *F. occidentalis* on chrysanthemum (Robb, 1989). In contrast, Bautista et al. (1996) reported that *F. occidentalis* fed and oviposited preferentially on TSWV-infected than on healthy romaine lettuce (*Lactuca sativa* var *longifolia* L.), jimson weed (*Datura stramonium* L.), and burdock (*Arctium lappa* L.) and that larval populations were 15–20% higher on TSWV-infected than on healthy plants.

Electronic penetration graphs indicate that soil applications of imidacloprid reduced the number and

duration of probing/feeding bouts by 77 and 92%, (Tables 2 and 3) on mustard and pepper plants, respectively, compared to thrips on non-treated plants. Reductions in the number and duration of feeding bouts have been associated with reduced acquisition and transmission of insect-transmitted plant viruses (Abraham and Epperlein, 1999; Boiteau and Singh, 1999; Collar et al., 1997; Gourmet et al., 1996; Harrewijn et al., 1998; Harvey et al., 1996; Woodford and Mann, 1992). Our results clearly indicate that imidacloprid reduced both the number and duration of probing/feeding bouts by *F. fusca*, as well as the proportion of plants that became infected with TSWV, when the number of viruliferous thrips was limited to 10 per plant. These findings indicate that imidacloprid may reduce the incidence of TSWV in field situations when the populations of viruliferous *F. fusca* are low to moderate. However, it is likely that the protective effects of imidacloprid will be compromised by high populations of viruliferous thrips, which may explain the inconsistent effects of imidacloprid on the spread of TSWV (Funderburk et al., 1990; McPherson et al., 1992; McPherson et al., 1998; Todd et al., 1996).

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