Transmission of Tomato Spotted Wilt Virus to Tomato Plants of Different Ages[1]

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Abstract Thrips (Thysanoptera: Thripidae) and mechanical transmissions of tomato spotted wilt virus (TSWV) to tomato (*Lycopersicon esculentum* Mill, cv. 'Sunny Hybrid') were investigated relative to plant age at the time of inoculation. In 1999, thrips and mechanical transmissions were compared between plants at 7, 14 and 28 d after germination under field exclusion cages. In 2000, thrips transmission was evaluated in plants at 7, 14, 21, 28, 35 and 42 d after germination, and mechanical transmission was evaluated in plants at 14, 21, 28, 35, 42 and 49 d after germination. Subsamples of thrips from flowers of TSWV-infected tomato used in 1999 transmission consisted of 59% *Frankliniella occidentalis* (Pergande), 34% *F. tricici* (Fitch), and subsamples of thrips collected from onion used in 2000 transmission consisted of 78% *F. occidentalis* and 19% *F. fusca* (Hinds). There was significant yield reduction resulting from early transmission of TSWV in the mechanical transmission test in 2000 ($P = 0.008$), but not in thrips transmission test in 2000 ($P = 0.62$). A reduction in the percent of TSWV-damaged fruit in late transmission was significant in the thrips transmission test ($P = 0.04$) but not in the mechanical transmission test ($P = 0.25$) in 2000. Lag time from virus transmission to symptom development or to a positive ELISA test was highly correlated to TSWV damaged fruit ($P < 0.001$ and $P < 0.001$, respectively) in the mechanical transmission test in 2000. The lag time of a positive ELISA in the thrips transmission test in 2000 correlated with the percentage of TSWV-damaged fruit ($P = 0.009$). In summary, early infection of TSWV to tomato plants resulted in lower yield and a higher percentage of TSWV-damaged fruits than late infection.

Key Words *Bunyaviridae, Tospovirus,* western flower thrips, flower thrips, tobacco thrips

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Tomato spotted wilt virus (TSWV) of genus *Tospovirus* in the family *Bunyaviridae* (Wijkamp et al. 1995) is an economically important virus in a wide range of crops worldwide (German et al. 1992). It was first detected in tomato, *Lycopersicon esculentum* Mill. (Brittlebank 1919), and characterized with necrotic spots on leaves, severe wilting and reduction in both quantity and quality of fruit yield (Moriones et al. 1998 and Riley and Pappu 2000). Diagnosis of TSWV infection is usually confirmed by enzyme-linked immunosorbent assay (ELISA) (Cho et al. 1988, Marchoux et al. 1991).

TSWV is naturally transmitted by only eight species of thrips (Thysanoptera: Thripidae) (Ullman et al. 1997) though mechanical transmission is possible under

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laboratory conditions (Kumar et al. 1993). Western flow thrips, *Frankliniella occidentalis* (Pergande), and tobacco thrips, *F. fusca* (Hinds), had been correlated with field infection of TSWV (Aramburu et al. 1997, McPherson et al. 1999, Riley and Pappu 2000) while flower thrips, *F. tritici* (Fitch), is a non-vector species (Eckel et al. 1996).

Management practices aimed at reducing thrips populations have been reported to reduce the incidence of TSWV and increase tomato yields (Riley and Pappu 2000). However, the time during the growing season that management tactics provide the most benefit has not been specifically determined. Additionally, the age of tomato plants most susceptible to TSWV has not been directly determined relative to thrips inoculation, but indirectly related to symptoms under the assumption of a uniform lag-time of symptom development from thrips transmission (Moriones et al. 1998). Tomato plants that were observed to have symptoms early in the season have reduced growth and yield compared to tomato plants that were first observed with symptoms late in the season (Fajado et al. 1997, Moriones et al. 1998).

We hypothesized that the infection of TSWV in tomato plants at an early age affects the yield of tomato to a greater extent than does later infection, and that both inoculation methods, mechanical and thrips, should provide similar results with respect to the relationship between time of inoculation and effect on yield. We tested this hypothesis under field conditions.

Materials and Methods

In a series of three experiments, we evaluated the yield effects of two methods of TSWV transmission, mechanical and thrips transmission, and plant age at infection (7 to 49 d after germination). (1) Mechanical and thrips transmission to tomato plants in field exclusion cages were conducted May through August 1999 to plant ages 7, 14 and 28 d after germination. (2) Thrips transmission was conducted March through June 2000 to plants in field exclusion cages at 7, 14, 21, 28, 35 and 42 d after germination. (3) Mechanical transmission was conducted March through June 2000 to plants under insecticides protection at 14, 21, 28, 35, 42 and 49 d after germination. A true check of non-inoculated plants was not used in our study because all protection methods were to be removed at a certain age when plants were too large for the field exclusion cage. Insecticide treatments also needed to be terminated before harvested, so even non-inoculated plants could be infected from the ubiquitous wild thrips population under natural field conditions.

Experiments were conducted in field plots located at the Coastal Plain Experiment Station, University of Georgia, Tifton, GA. The test plots were on 180 cm wide by 20 cm raised beds covered with black plastic mulch. Each row was treated with 98% methyl bromide 550 kg AI/0.4046 ha. Ten g of slow-release 14-14-14 fertilizer (Osmocote®, Scotts-Sierra Horticulture Products Co., Marysville, OH) was added to the base of each plant during transplanting. Plants were transplanted at 7 d after germination at a 90 cm interval for field exclusion cage experiments and a 60 cm interval for insecticide protection experiment.

Tomato plants. Tomato plants were 'Sunny Hybrid' (Asgrow Seed Co., Kalamazoo, MI) seeded in a thrips-free growth chamber (Percival Scientific Inc., Perry, IA, L:D 12:12, 26°C). Seven and 14-d-old plants had only cotyledons. Plants at 21 to 42 d from germination had true leaves but no flowers. Plants after 49 d from germination started producing flowers. There were six plants per each combination of age and

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transmission method except for mechanical inoculation in 1999 experiment; five and seven plants were used for the 7 d and 14 d treatments, respectively.

Exclusion cages. Field exclusion cages were 45 × 45 × 120 cm (length × width × height) in dimension made from an aluminum conduit pipe (2 cm diam) frame covered with screen bags. The screens with a replicate were made from white or ivory fine mesh chiffon (quality 3871, Shason Inc., Japan) with 40 cm strapped fasteners (Velcro®, Velcro USA Inc., Manchester, NH) opening at one corner. The bottom of the screens was sealed by weighing down with plastic tube sandbags around the frames. The screens were removed when plants were 63 d old.

Insecticide treatment. A mixture of 53.9 g AI/ha lambda-cyhalothrin (Karate 1EC®, Zeneca AG Products, Wilmington, DE) and 709.8 liter AI/ha methamidophos (Monitor 4L®, Bayer Corp., Kansas City, Kansas) was sprayed to eliminate and prevent thrips infestation. Plants in mechanical transmission test in 2000 were protected from natural thrips infestations by a combination of foliar application mixture of lambda-cyhalothrin and methamidophos and soil drench of imidacloprid (Admire 2F®, Bayer Corp., Kansas City, KS) at rate of 0.644 mL AI/liter water/plant, after transplanting. The combination of the above sprayed and systemic insecticides was reported to be highly effective against thrips and TSWV incidence in tomato (Riley and Pappu 2000). A mixture of λ-cyhalothrin and methamidophos was sprayed weekly until plants were 70 d old.

Mechanical transmission. Inoculum source for mechanical inoculation was collected from symptomatic tomato plants, which were verified by ELISA for the presence of TSWV. In the 1999 experiment, fresh leaves were used as inoculum. Three plants from each age in the 1999 experiment and 6 plants from each age in the 2000 experiment were mechanically inoculated as described in Kumar et al. (1993) except that the inoculum was applied to half of each leaf on each plant. Leaves from a TSWV-infected plant were collected and macerated with pre-chilled TSWV-inoculation buffer (0.1 M potassium phosphate and 0.01 M sodium sulfite) in a chilled mortar. Plants to be inoculated were dusted with carborundum, and inoculum was applied over and under the leaf surface. Carborundum was washed off the leaf surface with a water spray the next day. Plants in Experiment 3 were covered with brown paper bags after inoculation for 1 d, then carborundum dust was washed from the leaves.

Thrips transmission. Thrips in 1999 were collected from blossoms of TSWV infected tomato plants in a nearby field, approximately 50 m from the field cages, 1 d prior to inoculation, and placed in self-sealed plastic bags. Subsamples of these thrips consisted of 59% *Frankliniella occidentalis,* 34% *F. tritici,* and 25% viruliferous thrips. Approximately 20 thrips were placed in each 20-mL vial, and each vial was opened and placed next to the randomly selected tomato plants at selected plant ages. Approximately 72 h after initiating the inoculation access, both thrips-mediated and mechanically inoculated tomato plants were drenched with a mixture of the insecticides, λ-cyhalothrin and methamidophos.

Thrips used in 2000 were obtained from an onion field approximately 200 m from the field exclusion cages. Subsamples of these thrips consisted of 78% *F. occidentalis* and 19% *F. fusca* (Hinds). Thrips can only acquire the virus during their immature stages, and immature of *F. occidentalis* can optimally acquire TSWV at 21 h and have optimal inoculation access period of 43 h (Wijkamp et al. 1996). Immature of *F. occidentalis* and *F. fusca* were collected by an aspirator from the onion leaves. Twenty immature thrips were put in a plastic vial with TSWV-infected tomato leaves

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for 48 h (at 25°C and L:D 12:12) before being placed next to an assigned tomato plant. The tomato plants then were sprayed with a mixture of λ-cyhalothrin and methamidophos 7 d after thrips were released in the exclusion cages. Infected tomato leaves were collected from 4-wk-old mechanically-inoculated tomato plants previously confirmed positive for TSWV. The assumed percent viruliferous thrips was 33 to 35% based on the data of Wijkamp et al. (1995) and de Assis et al. (2002) for both *F. occidentalis* and *F. fusca.*

Plant measurements. In all experiments, each week after inoculation one leaflet from the third leaf from the terminal end of each plant was collected and placed in plastic bags. No leaf sample was collected from pre-inoculated plants because of the size of plants and the ensured TSWV-free condition of pre-inoculated plants by germination in a thrips-free growth chamber. Leaf samples were stored at 4°C while waiting to be tested for the presence of TSWV with double antibody sandwich ELISA (DAS-ELISA) (Agdia TSWV-DAS-ELISA Kit, Agdia Inc., Elkhart, IN). Plants were examined weekly for symptoms (necrotic spots, wilting, and stunting). Harvested fruit were weighed and graded by size and regularity of color and shape. TSWV-damaged fruit were characterized as fruit with uneven ripening (i.e., mottle, mosaic, concentric rings) and concentric scars. Remaining fruit were classified as normal.

Statistical analysis. Fruit yield and symptom expression were compared across treatments, i.e., method of inoculation and plant age at inoculation, using two-way ANOVA (Proc ANOVA, SAS Institute 1998) for thrips and mechanical transmission in 1999, and yield was correlated with the presence of TSWV using ELISA and symptom expression (Pearson's correlation, Proc CORR, SAS Institute 1998). Proc GLM (SAS Institute 1998) was used in the analysis of thrips and mechanical transmissions in 2000. All percentage values were arcsine-transformed before being analyzed.

Results and Discussion

Mechanical vs thrips transmission. Mechanical transmission was similar to thrips transmission in most of the inoculated tomato plant ages used in the 1999 test, with the exception of one age in each of the yield and TSWV-damaged fruit test categories. Thrips and mechanical transmissions in 1999 had no significant difference in terms of total fruit weight (813.0 ± 293 g and 707.8 ± 306 g, respectively, $F_{1,30}$ = 0.25, P = 0.61) and percent TSWV-damaged weight (68.2 ± 15.4% and 53.1 ± 11.7%, respectively, $F_{1,30}$ = 2.69, P = 0.11) average across inoculated ages at 7, 14, and 28 d. However, there were differences at the individual inoculated ages of 14 d (Fig. 1A) and at 7 d (Fig. 1B). Time required for symptom development between thrips and mechanical transmissions was not significant ($F_{1,30}$ = 0.25, P = 0.61), but the interaction between transmission methods and plant age was significant relative to the lag time required for symptom development ($F_{2,30}$ = 4.17, P = 0.02).

Yield reduction and inoculated ages. The earlier infection of TSWV to tomato plants resulted in lower total yield and higher percentage of TSWV-damaged fruits than later infection in several tests. Yield (total fruit weight) reduction in early transmission of TSWV was significant in mechanical transmission in 2000 ($F_{5,30}$ = 3.71, P = 0.008), but not in thrips transmission in 2000 ($F_{5,30}$ = 0.71, P = 0.62) (Fig. 2A), and reduction in percent of TSWV-damaged weight in late transmission was significant in thrips transmissions in 2000 ($F_{5,30}$ = 2.58, P = 0.04) but not in mechanical transmission in 2000 ($F_{5,30}$ = 1.39, P = 0.25) (Fig. 2B). The average total fruit weight and the average percent TSWV-damaged fruit were 2499.88 ± 963.1 g and 38.06 ± 12.4%,

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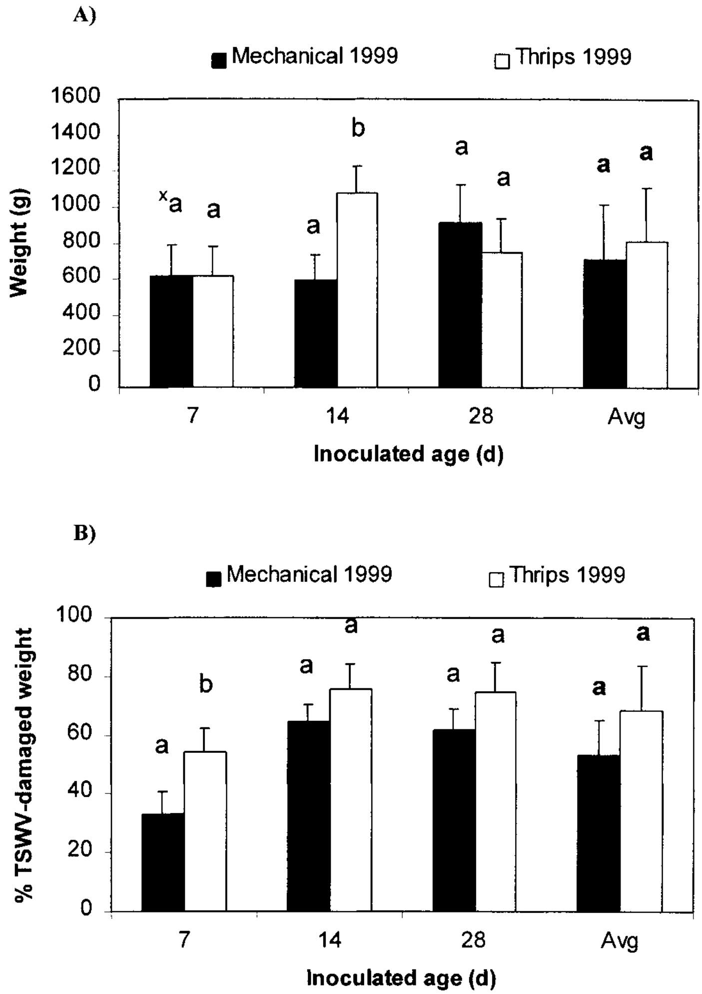

Fig. 1. Fruit yields from tomato plants inoculated with tomato spotted wilt virus (TSWV) by thrips and mechanical inoculation at age 7, 14, and 28 d after seeding and an average across these three ages in May-July 1999. (A) Total fruit weight (grams) and (B) percent TSWV-damaged weight. [x]Same letters between thrips and mechanical inoculation of each age indicate non-significant difference between means (LSD, $P > 0.05$).

respectively, in the thrips transmission test in 2000 and 1185.17 ± 955.5 g and 13.37 ± 8.0%, respectively, in the mechanical transmission test in 2000.

Symptom expression. In these tests, ELISA detected TSWV before observing necrotic spots, wilting, and stunting in the test plants (Fig. 3). The average lag time from inoculation to a positive test for ELISA over all mechanical and thrips transmis-

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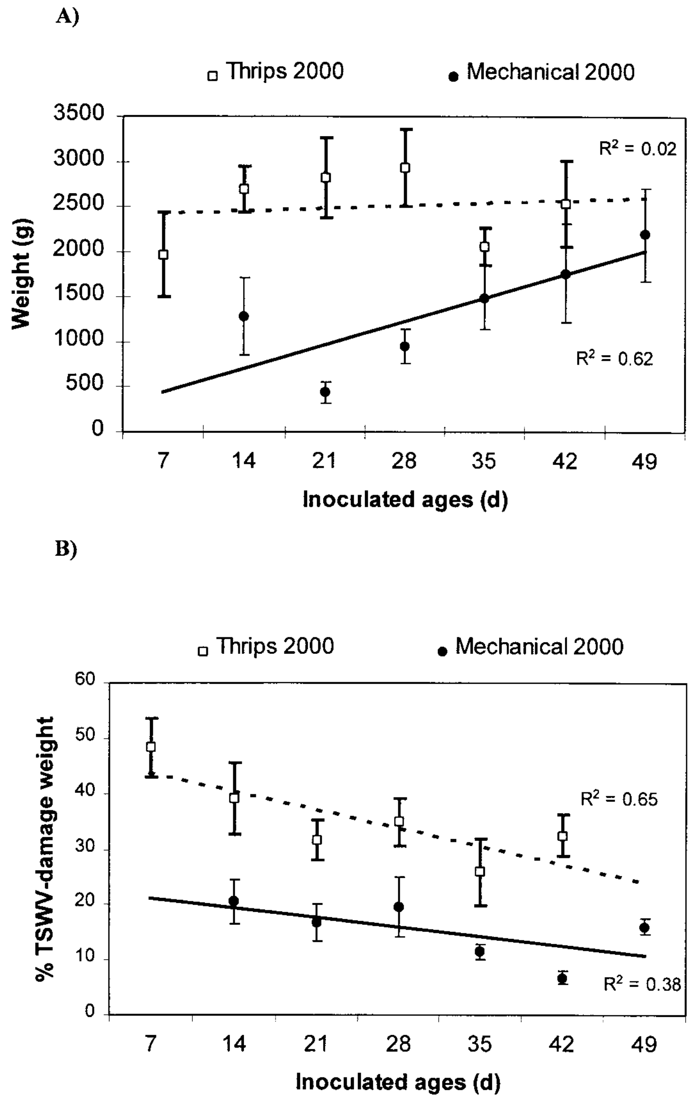

Fig. 2. Fruit yields from tomato plants inoculated with tomato spotted wilt virus (TSWV) by thrips at age 7, 14, 21, 28, 35 and 42 d after seeding and by mechanical inoculation at age 14, 21, 28, 35, 42 and 49 d after seeding in March-June 2000. (A) Total fruit weight (grams) and (B) percent TSWV-damaged weight.

sion tests were 30.3 ± 24.1 d and 34.1 ± 20.7 d, respectively. The average lag time from inoculation to symptom development over all mechanical and thrips transmission tests were 33.5 ± 18.0 d and 42.4 ± 16.1 d, respectively. Symptom lag time ranged from a minimum of 7 d to a maximum of no symptom development but a positive test

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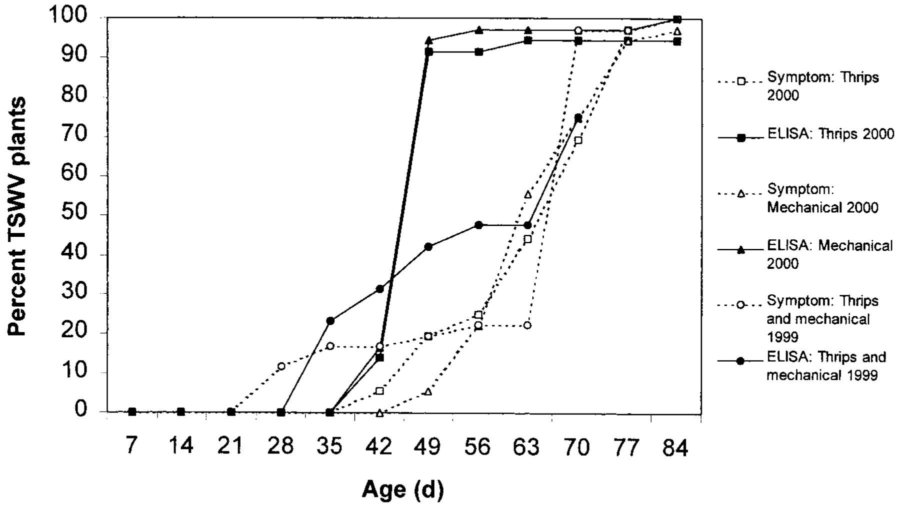

Fig. 3. Percent of tomato plants infected with tomato spotted wilt virus (TSWV) by thrips and mechanical transmission identified by symptoms (dotted lines) and DAS-ELISA (solid lines) every 7 d after inoculation. Thrips 2000 was the average across thrips-transmitted plants at age 7, 14, 21, 28, 35 and 42 d after seeding in March-June 2000. Mechanical 2000 was the average across mechanical inoculated plants at age 14, 21, 28, 35, 42 and 49 d after seeding in March-June 2000. Thrips and mechanical 1999 was the average across both thrips and mechanical transmitted plants at age 7, 14 and 28 d after seeding in May-July 1999.

for ELISA on the last sample date (Fig. 4). Lag time from transmission to development of symptoms or to a positive test with ELISA significantly correlated with inoculated age in mechanical transmission in 2000 ($r = 0.33$, $P = 0.04$ and $r = 0.34$, $P = 0.04$, respectively), but symptom lag time did not significantly correlate with inoculated age in the exclusion-caged experiments with both thrips and mechanical transmission in 1999 and thrips transmission in 2000. Symptoms on the foliage corresponded more with the removal of screen cage netting when plants were 63 d old than inoculated age, especially in thrips and mechanical transmission in 1999 (Fig. 3). Apparently, shading suppressed the development of symptoms.

Lag time from transmission to develop symptom or to positively test with ELISA did not significantly correlate to total fruit weight in either thrips transmission in 2000 ($r = -0.23$, $P = 0.18$, and $r = -0.16$, $P = 0.35$, respectively) or mechanical transmission in 2000 ($r = -0.23$, $P = 0.17$ and $r = -0.22$, $P = 0.20$, respectively). However, both lag times in the mechanical transmission test in 2000 and the lag time of a positive ELISA in thrips transmission test in 2000 were negatively correlated with the percentage of TSWV-damaged fruit weight ($r = -0.76$, $P < 0.001$; $r = -0.74$, $P < 0.001$; and $r = -0.44$, $P = 0.009$, respectively). Thus, inoculated plants with a shorter duration time before foliar symptom development resulted in higher levels of TSWV-damaged fruit in these tests.

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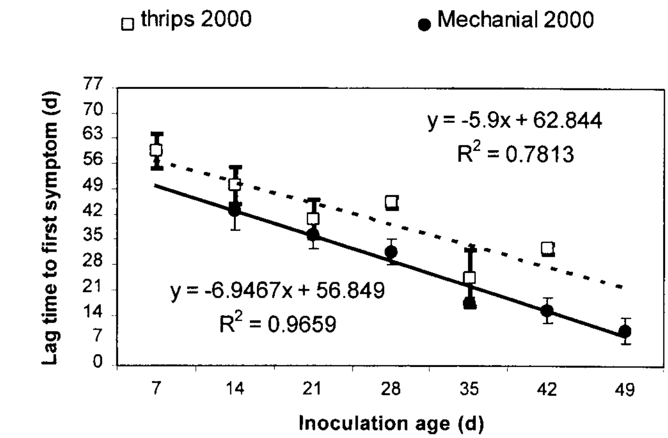
A)



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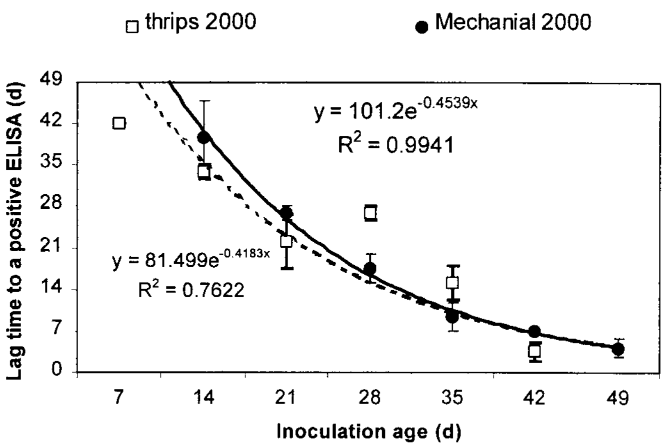

Fig. 4. Lag time to (A) first symptom and (B) a positive DAS-ELISA from inoculation ages of tomato plants infected with tomato spotted wilt virus (TSWV) by thrips and mechanical transmission tests in March-June 2000.

The hypothesis that early infection results in greater yield loss than later infection was supported by the data from both thrips and mechanical transmissions in 2000. However, the pattern of response was slightly different depending on transmission methods as well as exclusion methods of natural thrips populations. Although there was variable symptom intensity across the different field experiments, the trend of greater yield loss occurring with the earliest inoculations was evident in all experiments. Commercial tomato transplants are usually at least 2 true leaves, so the yield data in this study can be adapted to commercial growing of tomato by concentrating

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on yield data of TSWV inoculation at 21 d or older. If we omit the variation of inoculation at 14 d or younger (no true-leaf plants), the yield data of mechanical transmission in 2000 provided evidence of a strong reduction in yield with earlier transmission of TSWV (Fig. 2A).

Thus, the prevention of thrips inoculation early in the tomato-growing season needs to be emphasized in TSWV management programs in order to reduce the impact of TSWV on yield. Several factors could influence the yield of tomato infected with TSWV. Virus isolates and competency of each thrips population could vary from one to another (Roca et al. 1997, van de Wetering et al. 1999). Mechanical inoculation of TSWV to the youngest plants was apparently less effective than thrips transmission at the same age. Mechanical inoculation to tomato plants at 7 d caused a severe plant wound response and thus variable inoculation efficiency. Mandal et al. (2001) commented that with a young plant, mercaptoethanol as antioxidant in buffer, and non-destructive abrasion increased efficiency of TSWV mechanical inoculation of peanut. Mechanical inoculation may have inflicted serious damage to plant tissue and inhibited seedling growth. Inoculated plants with only one pair of leaves, especially less than 28 d old, had lagging growth compared to non-inoculated plants. The inoculated leaves usually developed premature wilting either from carborundum abrasion or from infection. The rapid death of leaf tissue could have resulted in the unsuccessful inoculation in some plants (3 of 18 plants in 1999 inoculation and 2 of 36 in 2000 inoculation).

One observation from these experiments was that symptoms may not always correspond closely to the presence of virus based on ELISA. Some plants tested positive for TSWV by ELISA without symptom expression. Even so, the yield response results agree with Moriones et al. (1998) in that earlier symptomatic plants produce less yield than later symptomatic plants. A notable effect was that symptoms developed rapidly across all treatments after the screen cages were removed, which was a source of shading. The infection of TSWV after removal of screens and termination of insecticide application occurred when fruits were mature and ready to harvest. Perhaps the most interesting phenomenon observed in these experiments was that the lag time between inoculation and symptom expression in the foliage was negatively correlated with the percentage of TSWV-irregular ripened tomatoes. This result would be consistent with TSWV-irregular ripening being caused by more inoculation occurring in the later age plants in these tests up to 49 d after germination, even though the yield is higher at the later age of inoculation. Based on these data we think that two distinct curves for the relationship of TSWV inoculation and tomato are needed, i.e., one for yield response and one for irregular ripening of tomato.

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