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Effect of plant age at time of infection by tomato spotted wilt tospovirus on the yield of field-grown tomato

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Abstract

Naturally infected tomato plants that expressed tomato spotted wilt virus symptoms at 24, 38, 45, 60, 67, and 74 days after transplanting were monitored for production in an experimental crop grown in the open from May to September in northeastern Spain. Plants were tagged, tested for tomato spotted wilt virus infection by enzyme-linked immunosorbent assay, and data on symptom expression and yield were individually recorded. Plants that developed symptoms at 24, 38, or 45 days after transplanting yielded significantly less and produced fewer and smaller tomatoes than those that developed symptoms at 60, 67, and 74 days after transplanting. These later infected plants showed similar patterns of production with maximum yields between 27 July and 17 August, when most fruit was harvested. Production components such as fruit number per plant, yield of mature fruit per plant, or fruit weight increased the older the plants were when first symptoms were exhibited. However, marketable fruit production was drastically decreased by tomato spotted wilt virus infection, due to abnormal ripening of mature fruit in infected plants. Little and no significantly different amounts of marketable fruit were produced, irrespectively of plant age at time of symptom expression. Implications for spotted wilt management in tomato are discussed.

Introduction

Tomato spotted wilt tospovirus (TSWV) occurs worldwide and causes severe economic losses in many ornamental and vegetable crops (Reddy & Wightman, 1988; German et al., 1992; Goldbach and Peters, 1994). The virus is common across northeastern Spain, where it annually threatens tomato (*Lycopersicon esculentum* Mill.) crops and is the limiting factor of production in important growing regions (Laviña et al., 1996). Due to the severity of TSWV epidemics, tomato production has been abandoned in some areas.

TSWV is transmitted by several species of thrips (*Thysanoptera: Thripidae*) of which the western flower thrips (WFT), *Frankliniella occidentalis* Pergande, is one of the most important (German et al., 1992). Management of the TSWV is difficult due to its wide host range and the polyphagous feeding of its vector (Yudin et al., 1986; Edwardson and Christie, 1986), especially for outdoor crops. The widely used practice of controlling thrips with insecticides is inefective in controlling TSWV (Cho et al., 1989) and causes environmental problems from residual chemical released. Resistance to TSWV has been described in several *Lycopersicon* species and breeding programs have been conducted to incorporate the resistance genes into cultivated tomatoes (Paterson et al., 1989; Stevens et al., 1992, 1995). Recently, TSWV resistant tomato cultivars have become commercially available which can reduce the economic problems caused by TSWV in the short to medium term. The question is how durable will the current forms of resistance be when they are exposed to variants of TSWV that may be present in natural virus populations over a period of time (Roca et al., 1997). Selection pressure can lead to the appearance of resistance breaking strains as observed in oth-

Figure 1. Abnormal colouration on the surface of fruits formed on tomato spotted wilt virus infected plants that occurs during ripening.

er pathosystems (Pelham et al., 1970; Adams, 1991; Pink et al., 1992). Therefore, management of spotted wilt through crop management strategies should not be discarded. In addition, the growing of tomato cultivars that do not incorporate TSWV resistance, but are of high economic value in local markets, strongly depends on the ability to control this virus through crop management. An extensive knowledge of TSWV epidemiology in endemically affected regions is needed for appropriate control measures to be recommended.

The objective of this study was to illustrate one of the aspects that should be considered to support decisions made to control TSWV epidemics in tomato crops. This paper reports on the yield losses caused by TSWV in tomato grown in natural field conditions depending on plant age at time of first TSWV symptom expression. The knowledge of losses caused by tomato spotted wilt in individual plants will contribute to the adoption of appropriate measures to control the disease. Information obtained from this study is essential in developing models for making strategic management decisions (Jeger and Chan, 1995) and hence reduce the losses caused by TSWV to tomato crops.

Materials and methods

Studies were conducted in 1995 at the Cabrils experimental station of the Institut de Recerca i Tecnologia Agroalimentàries (IRTA) located in the Mediterranean coastal area north of Barcelona (Spain). Natural infection by TSWV was monitored in an experimental plot of field-grown pole tomatoes for fresh market where 3000 tomato seedlings (cv. Leopardo) were transplanted on 15 May. Plants were arranged in rows with 0.8 m between rows and 0.5 m between plants in a row. The crop was maintained following standard commercial procedures, although plants were not sprayed with insecticides to promote a natural infection of TSWV from local sources. Symptoms of TSWV infection in tomato plants are distinctive and are expressed quite rapidly one or two weeks after thrips inoculation, depending on plant growth stage and climate conditions (E. Moriones, unpubl.). A number of plants that first exhibited symptoms of TSWV infection at different growth stages were randomly selected and individually tagged for further studies (Table 1). Time of symptom expression and not of virus infection was considered in this study because this is what a trained grower can directly assess in the field without the need of any laboratory support. Control asymptomatic plants were also tagged in the first harvesting date. An infection by TSWV in the selected plants was tested by DAS-ELISA, as described previously (Laviña et al., 1996). Mature tomato fruits were harvested individually from each tagged plant eight times, beginning 24 July and continuing through 7 September 1995 (24 and 27 July, 3, 10, 17, 24, and 31 August, and 7 September). At the last harvest, all remaining immature tomato fruits were also collected. Fruits were evaluated visually, counted and weighed. Following commercial standards, fruits were classified as marketable only when no external damage was observed. Fruit that expressed TSWV symptoms on their surface (abnormal colouration, necrotic spots or rings) (Figure 1) were separated and marketable fruit were counted and weighed.

Statistical analysis was carried out by means of a one-way analysis of variance test, followed by Tukey's multiple range test to detect differences among treatments (SAS Institute, 1990). Yield losses per plant were modelled as a function of time of symptom expression based on the equation $y = m \exp(-nt)$ proposed by Madden and Nutter (1995), by nonlinear regression analysis (SAS NLIN procedure) (SAS Institute, 1990). In this equation t is time of symptom expression, y is the per-plant loss, and m and n are constants that characterize the yield loss in the model: m is the per-plant loss if infection occurs at $t = 0$, and n represents the decline in loss as time of infection is delayed.

Table 1. Time of first symptom expression, growth stage, and number of plants monitored in six groups of plants naturally infected by tomato spotted wilt virus selected at different times of an epidemic

Group	Time of first symptom expression		Growth stage at symptom expression	Number of plants monitored
	Date	Days after transplanting		
1	8 June	24	1st-2nd inflorescence	11
2	22 June	38	3rd inflorescence	20
3	29 June	45	4th-5th inflorescence	19
4	14 July	60	6th-7th inflorescence	17
5	21 July	67	8th inflorescence	12
6	after 28 July	74	9th inflorescence-end	18

Table 2. Yield of mature and immature fruit per plant in plants of groups 1 to 6 that first exhibited tomato spotted wilt virus symptoms at 24, 38, 45, 60, 67, and 74 days after transplanting, respectively

Group	Mature fruit[a]				Not-mature fruit[a]	
	Fruit number/ plant	Yield (g)/ plant	Fruit weight (g)	Yield (g) marketable fruit/plant	Fruit number/ plant	Yield (g)/ plant
1	2.6 a[b]	255.0 a	57.9 a	17.3 a	1.2 a	64.5 a
2	9.2 b	628.5 ab	60.0 a	169.5 ab	3.6 ab	195.0 ab
3	14.0 c	1048.8 b	72.3 a	260.0 ab	4.4 ab	285.5 ab
4	20.7 d	2425.3 c	116.4 b	263.8 b	3.8 ab	223.5 ab
5	24.5 d	3271.3 d	133.3 b	182.5 b	5.7 ab	303.3 ab
6	28.6 d	3035.3 d	128.1 b	315.8 b	6.7 b	379.4 b

[a] mature fruit were collected on 24 and 27 July, 3, 10, 17, 24, and 31 August, and 7 September. Immature fruit were collected on 7 September. Values are mean for the plants monitored.
[b] values followed by the same letter within a column are not significantly different (Tukey's multiple range test at the 5% level).

Results

Symptoms

Typical TSWV symptoms (Best, 1968) were observed in plants monitored during the experiment. Tomato plants expressing TSWV symptoms at an early growth stage showed a dramatic stunting and abortion of new inflorescences. The fruits were small and usually showed necrotic spots or rings on their surface; if ripening occurred, abnormal colouration was shown. Some of these plants formed axillary asymptomatic shoots that growers usually maintain as main shoot, that could form inflorescences and tomatoes that were usually small and matured late in the season. When TSWV symptoms developed in tomatoes at later growth stages, symptoms were observed in young leaves and usually tended to progress to an apical necrosis; fruit were either symptomless or developed abnormal colouration during ripening (Figure 1), with few fruits exhibiting necrotic spots or rings. The older the plant at the time of initial symptom expression, the fewer the number of fruit with necrotic symptoms.

Although symptomatic plants were selected for infection by TSWV only, superinfection during the period monitored by other viruses known to occur in the area could not be excluded. However, surveys of tomatoes grown in this area (Laviña et al., 1996) indicated that mixed infections were very rare during this period of the growing season. In addition, symptoms other than those of TSWV infection were not observed in any plant in the plot monitored.

Effect of TSWV on fruit yield

Data on mature fruit collected from individual plants indicated that significant differences ($P < 0.05$) occurred among groups, depending on plant age at time of symptom expression. The total number of fruits produced per plant throughout the season varied from 2.6 to 14.0 for plants that exhibited symptoms during the first 45 days after planting (group 1 to 3, Table 1) which was significantly less than the 20.7 to 28.6 produced by

Table 3. Mean mature fruit yield loss in plants from groups 1 to 6 that first exhibited tomato spotted wilt virus symptoms at 24, 35, 45, 60, 67, and 74 days after transplanting, respectively, and nonlinear regression analyses of yield losses versus time of symptom expression

Yield loss[a]	Group					
	1	2	3	4	5	6
	0.95	0.87	0.78	0.49	0.31	0.35

Nonlinear regression analysis [y = *m* exp (-*nt*)] [b]

Parameters	Parameter estimate	Asymptotic standard error	Asymptotic 95% confidence interval		r^{*2} [c]	Residual pattern[d]
			Lower	Upper		
m	1.0299	0.0906	0.7781	1.2816	0.89	–
n	0.0205	0.0039	0.0095	0.0316		

[a] mean mature fruit yield loss was calculated as a proportion of the maximum per-plant mature fruit yield obtained in the trial.
[b] model parameter were estimated by nonlinear regression (SAS NLIN, SAS Institute 1990); time was arbitrarily considered t = 0 when first symptomatic plants were tagged.
[c] r^{*2}, coefficient of determination of correlation of predicted values against observed values.
[d] –, absence of pattern in the plots of the residuals of nonlinear regression over time.

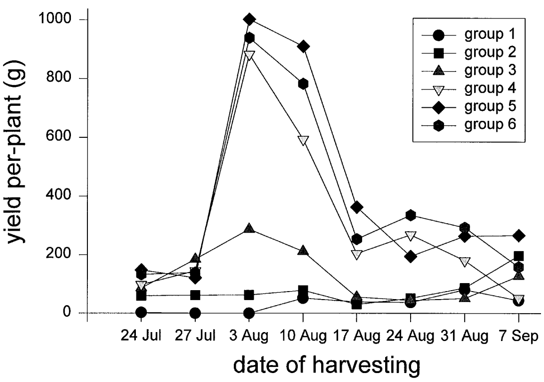

Figure 2. Mean yield of mature tomato fruit obtained per-plant within groups 1 to 6 of plants that exhibited initial tomato spotted wilt virus symptoms at 24, 38, 45, 60, 67, and 74 days after transplanting, respectively, at each harvesting date.

plants that exhibited symptoms later (Table 2). A significantly lower yield per plant occurred in plants from groups 1 to 3 than in plants from groups 4 to 6 (255–1048 g versus 2425–3035 g, Table 2). In addition, the average weight per fruit ranged from 57 to 72 g in the first case which was significantly lower than the 116 to 128 g from plants of groups 4 to 6. However, marketable tomato fruit yields did not correlate with total yields (Table 2) since most fruits formed on infected plants (over 85% of fruits, data not shown) exhibited an abnormal colouration on their surface during ripening (Figure 1). Very low yields of marketable fruit were harvested from the plants irrespectively of plant age at the time of symptom expression (Table 2). No significant differences occurred between plant groups in the amount of immature fruit that remained on plants after the last harvesting date.

Estimation of yield losses

During 1995, the TSWV epidemic was so severe that all plants selected as control had become infected by the end of the experiment. Per-plant yield losses therefore refer to the maximum per-plant yield in the trial, so that the relationship between time of symptom expression and yield loss can be studied (Table 3). Data were adjusted to the function proposed by Madden and Nutter (1995), and showed that mature fruit yield was significantly affected by plant age at the time of first symptom expression. The older the plants were before they exhibited TSWV symptoms the lower the resultant yield loss. Although a higher total production occurred in late infected plants, the results showed that most fruits were unmarketable due to abnormal ripening (Table 2).

Effect of TSWV on time of production

Figure 2 shows yield of mature fruit in plants of groups 1 to 6 (Table 1) at each harvesting date. Significantly higher yields ($P < 0.05$) were recorded in plants of groups 4 to 6 when harvested on 3, 10, 17, and 24 August. Maximum yields in groups 3 to 6 were recorded between 27 July and 17 August, when most fruit was collected. A similar maximum was not observed in groups 1 and 2.

Discussion

The age at which plants are infected is often an important factor in determining loss of yield in economically important crops (Bovey et al., 1957; Scott et al., 1977). For instance, infection of cantaloupe (*Cucumis melo* L.) plants by zucchini yellow mosaic virus (ZYMV) during vegetative and early flowering stages caused up to 94% reduction in marketable fruit, whereas no effect was observed if plants were infected after fruit set (Blua and Perring, 1989). This study showed that most yield components measured were dramatically affected by plant age at the time of TSWV initial symptom expression. Hence, significantly lower number of fruits, fruit weight, and yield were recorded in plants expressing symptoms early in development than those at a more mature stages, and a function was obtained for predicting a baseline of yield losses based on time of initial symptom expression (Table 3). However, in contrast to other viral diseases (Agrios et al., 1985; Blua and Perring, 1989; Avilla et al., 1997), the quality of production was dramatically altered by TSWV infection even in late infected plants. Little or no significant difference in marketable fruit yield was obtained in every case, regardless of plant age when TSWV symptoms were first observed.

We have shown that management strategies directed at delaying infection useful in other virus/host combinations to increase marketable fruit production such as for cucumber mosaic virus in pepper (Agrios et al., 1985; Avilla et al., 1997) or ZYMV in cantaloupe (Blua and Perring, 1989) will not be effective for TSWV in tomato, at least in the period considered. As exemplified in Figure 2, tomato production practices in the area lead to most fruits being harvested from plants before mid-late August in tomatoes transplanted between late April and mid May. Therefore, control methods for avoidance of TSWV infection before these dates would result in reduced crop losses, and, hence, strategies to prevent virus infection should be investigated, e.g., application of horticultural oils or film forming products (Allen et al., 1993), use of thrips-repellent mulches (Greenhough et al., 1990), or floating row covers (Perring et al., 1989).

Information presented here clearly illustrates the devastating effects of TSWV infection in tomato plants. Data provided by this study offers valuable information to support decisions in management practices to control TSW epidemics in tomato. The knowledge of loss per plant could be linked, if available, with information on disease progress to predict loss for the whole crop (Madden and Nutter, 1995) as a tool to make strategic decisions in integrated control programs for TSWV.

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