Prevalence of Verticillium Wilt of Tomato and Virulence of *Verticillium dahliae* Race 1 and Race 2 Isolates in Western North Carolina

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ABSTRACT

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Verticillium wilt was confirmed in 56% of 108 tomato fields surveyed (56.5% of 65.6 ha) in western North Carolina in 1976. Estimated disease incidence in the surveyed region was 9.2%. Eighty-nine of 96 *Verticillium dahliae* isolates recovered from susceptible cultivars in the survey were race 1; seven were race 2. Six race 2 isolates came from fields not previously cropped with race 1-resistant cultivars. In field tests, mean yields were reduced in susceptible cultivars Manapal and Walter and race 1-resistant cultivars Flora-Dade and Monte Carlo, respectively, by as much as 39.9, 47.1, 3.5, and 6.5% by race 1 isolates and 10.3, 31.2, 19.3, and 22.8% by race 2 isolates.

Verticillium wilt of tomato (*Lycopersicon esculentum* Mill.) is a vascular wilt disease caused by *Verticillium dahliae* Kleb. (microsclerotial form of *V. albo-atrum* Reinke & Berth.) and *V. albo-atrum* (dark mycelial form) (5). Both pathogens infect many plant species, including trees, vegetables, field crops, ornamentals, and weeds (14). Verticillium wilt has been a serious problem on tomatoes in California (9), Florida (8,12), and Ohio (1). Yield losses of 30–69% have been observed on susceptible cultivars (2,8,12).

Effective control of this disease has been obtained by planting resistant cultivars (12). In 1951, Schaible et al (19) reported a high level of resistance to Verticillium wilt in a small-fruited, wild Peruvian cherry tomato (*L. esculentum* var. *cerasiforme* Gray 'Peru Wild') (Utah 655). This resistance, conferred by a single dominant gene (*Ve*), has been incorporated into many current tomato cultivars. In 1957, an isolate of *V. dahliae* from tomato in California and an isolate of *V. albo-atrum* from potato (*Solanum tuberosum* L.) in Canada were reported pathogenic on Loran Blood, a tomato cultivar with the *Ve* gene (18). Since then, similar isolates of this new race (race 2) have been discovered in Ohio (1), California (9,10), and several European countries (7,16,21).

Isolates of *V. dahliae* and *V. albo-atrum* pathogenic on susceptible tomato cultivars (lack *Ve* gene) but nonpathogenic on race 1-resistant cultivars (possess *Ve* gene) have been designated race 1 or tomato strain 1, and isolates pathogenic on both susceptible and race 1-resistant cultivars have been designated race 2 or tomato strain 2 (9,10). Race 2 has become widespread in California, and in fields infested with race 2, yield losses of 25% have been estimated for race 1-resistant cultivars when disease incidence was 100% (9).

A survey of commercial, fresh-market tomato fields was conducted in 1976 to assess the prevalence and severity of Verticillium wilt on tomato production in western North Carolina. Disease incidence, symptom severity, crop acreage, cultivar grown, and cropping history were recorded. Isolates of *V. dahliae* were obtained from infected tomato plants in the survey fields. These isolates were tested in the greenhouse and the field for differences in pathogenicity and virulence on susceptible and race 1-resistant tomato cultivars. A preliminary account of this work has been published (4).

MATERIALS AND METHODS

Survey. One hundred eight fresh-market tomato fields in 11 western North

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Carolina counties were surveyed for Verticillium wilt in 1976. Fields were selected randomly and surveyed once during the latter half of the growing season, 20 July–12 August, when foliar symptoms were prominent. Each field was divided into four sections, and 50 consecutive plants from the middle row of each section (200 plants per field) were examined visually for Verticillium wilt symptoms. The number of infected plants in each row of 50 plants was recorded and percent disease incidence was calculated for each field and for the 11-county region.

Isolate screening. Ninety-four single-spore isolates of *V. dahliae* collected during the Verticillium wilt survey, an isolate (CF) from Cocke County, TN, and an isolate (111B) from North Carolina were screened in the greenhouse for differences in pathogenicity on three susceptible tomato cultivars (Manapal, Rutgers, and Walter) and on three race 1-resistant cultivars (Flora-Dade, Monte Carlo, and Tropic). Fifty-eight of the survey isolates and isolates CF and 111B were screened in a greenhouse at North Carolina State University, Raleigh, during January and February 1977. The remaining 36 survey isolates were screened in a greenhouse at the Mountain Horticultural Crops Research Station, Fletcher, NC, in June and July 1977.

Inoculum for each isolate was prepared using two 14-day-old cultures on potato-dextrose agar (PDA) plates blended (low speed for 60 sec) with 40–50 ml of sterile distilled water to make a thick slurry. Tomato seedlings 10–14 days old (first true leaf stage) were inoculated by immersing roots in the inoculum slurry for 10–15 min. Seedlings immersed in a pathogen-free agar slurry were used as uninoculated controls. The seedlings were then transplanted to flats containing a potting medium of pasteurized vermiculite and fluffed peat (1:1, v/v) with added dolomitic lime, fertilizer, and micronutrients. Treatments were arranged in a split-plot design replicated in two blocks with isolates (flats) as the main plots. All seedlings within a given flat were treated with the same pathogen isolate or pathogen-free slurry. Cultivars were randomized within each flat with six rows (subplots) of seven plants (Raleigh test) or five plants (Fletcher test) per flat. Ambient air temperature in the greenhouses at Raleigh and Fletcher during the experiments ranged from 18 to 32 C (avg. 24 C) and from 21 to 40 C (avg. 29 C), respectively. The experiment was conducted twice at both locations.

The criterion for pathogenicity on each tomato cultivar was development of typical foliar symptoms of Verticillium wilt (chlorosis, necrosis, and wilting) on cotyledons and true leaves within 28 days of inoculation. Isolates pathogenic on susceptible cultivars (lack the *Ve* gene) but nonpathogenic on race 1-resistant cultivars (possess the *Ve* gene) were designated race 1. Isolates pathogenic on both susceptible and race 1-resistant cultivars were designated race 2.

Pathogenicity of race 1 and race 2 isolates in the greenhouse. Pathogenicity and virulence of two tomato race 1 isolates (20B and CF) and three tomato race 2 isolates (50A, 91A, and 105A) of *V. dahliae* from North Carolina and Tennessee were compared along with a race 2 isolate (S89-4) from California on two susceptible tomato cultivars (Manapal and Walter) and two race 1-resistant tomato cultivars (Flora-Dade and Monte Carlo). Flora-Dade and Walter are determinate and Manapal and Monte Carlo are indeterminate cultivars. Seedlings of each cultivar were root-dip-inoculated 14 days after seeding and transplanted into flats containing a pasteurized potting medium of vermiculite, peat moss, sand, and loam soil (10:12:10:3, v/v) plus added lime, micronutrients, and fertilizer. Inoculum was prepared as described before. For each pathogen isolate, four and eight seedlings (in 1978 and 1979, respectively) of each cultivar were inoculated with the same isolate. Uninoculated controls (seedlings dipped in PDA suspensions) were included. The seedlings were grown for 35 days after inoculation in a greenhouse maintained at 20–30 C. The test was conducted in 1978 and repeated in 1979.

The criterion for isolate pathogenicity on each tomato cultivar was development of typical foliar symptoms of Verticillium wilt. Isolate virulence (severity of foliar symptoms) was estimated using a scale of 0–5, where 0 = no symptoms, 1 = chlorosis and wilting of cotyledons, 2 = chlorosis and wilting of first true leaf, 3 = symptoms on lower 50% of the foliage, 4 = symptoms on 51 –100% of the foliage, and 5 = dead plant.

Pathogenicity of race 1 and race 2 isolates in the field. The influence of selected race 1 and race 2 isolates on foliar symptom development and tomato yield was examined in the field in 1977 and 1978. In 1977, two race 1 isolates (CF and 20A) and three race 2 isolates (50A, 59B, and 105A) were tested on two susceptible cultivars (Manapal and Walter) and two race 1-resistant cultivars (Flora-Dade and Monte Carlo). Inoculum of each isolate was prepared as described before. Thirty-day-old seedlings of each cultivar were inoculated with 3.9×10^7 conidia and 60 microsclerotia (ms) per plant. Inoculum was poured into two holes 3 in. deep that were cut into the potting medium for each seedling. Seedlings were transplanted into fumigated (67% methyl bromide-33% chloropicrin mixture at 392 kg/ha) Elsinboro loam soil in the field 5 days after the initial inoculation. Each seedling was reinoculated with an additional 3×10^3 ms by pouring the inoculum into the soil around each seedling during transplanting. Treatments were arranged in a randomized complete block design with four blocks. Each treatment consisted of four seedlings of a single cultivar spaced 46 cm apart in rows 122 cm apart. Each group of four seedlings was either inoculated with one of the five *V. dahliae* isolates or was an uninoculated control treatment.

In 1978, race 2 isolate 50A and race 1 isolates CF and 20B were used. Inoculum of each isolate was prepared as in 1977, but ms were partially isolated and concentrated by sieving the comminuted cultures through a 150-μm sieve over a 38-μm sieve. The ms collected on the 38-μm sieve were quantified and used as inoculum. Twenty-day-old seedlings were initially inoculated with 1×10^4 ms/plant and reinoculated 14 days later with an additional 1.2×10^5 ms/plant when transplanted into a fumigated field of Elsinboro loam soil. Treatments were arranged in a split-plot design replicated in four blocks with isolates as the main plots. Cultivars (subplots) were arranged randomly within each main plot. Each subplot consisted of four seedlings of a single cultivar spaced 61 cm apart. Subplots were spaced 152 cm apart and main plots were spaced 213 cm apart.

Standard cultural and pest control practices for determinate tomatoes were used on all cultivars both years (13). All fruit showing red color were harvested and weighed weekly for 9 and 10 wk (end of the growing season) in 1977 and 1978, respectively. Severity of foliar symptoms (scale of 0–10, where 0 = no symptoms, 1 = symptoms on 10% of the foliage, 2 = symptoms on 20% of the foliage, etc., and 10 = dead plant or severe chlorosis, necrosis, and wilting on 100% of the foliage) was estimated 79 days after transplanting in both years. Data were analyzed using the Statistical Analysis System (3) at the Triangle Universities Computation Center, Research Triangle Park, NC. Differences between races and isolates on each cultivar were analyzed by analysis of variance and by partitioning the degrees of freedom for treatments into single degrees of freedom based on a set of mutually orthogonal contrasts (20). Sums of squares and *F*-statistics were calculated for each contrast.

In 1977, means for yield data were based on total fruit yield per four-plant plot, then converted to metric tons per hectare (t/ha). In 1978, yield means were based on total yield per plant, then converted to t/ha, because hail destroyed about 12.5% of the plants 7 days after transplanting to the field.

RESULTS

Survey. Verticillium wilt was confirmed in 56% of 108 fields surveyed or 56.5% of 65.6 hectares surveyed. Estimated disease incidence for the 11-county region was 9.2%, but estimated disease incidence for individual fields ranged from 0 to 100%. Four disease incidence classes representing

Table 1. Symptom severity for susceptible and resistant tomato cultivars inoculated in the greenhouse with races 1 and 2 of *Verticillium dahliae*[x]

		Symptom severity[y]											
		Susceptible cultivars						Resistant cultivars					
		1978			1979			1978			1979		
Race	Isolate	Manapal	Walter	Avg.	Manapal	Walter	Avg.	Flora-Dade	Monte Carlo	Avg.	Flora-Dade	Monte Carlo	Avg.
···	Control	0.0 a[z]	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a
1	20B	4.3 d	4.5 c	4.4 d	3.0 b	4.1 d	3.6 d	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a
	CF	···	···	···	3.6 b	2.8 bc	3.2 cd	···	···	···	0.0 a	···	0.0 a
2	50A	2.0 b	2.8 b	2.4 b	2.9 b	2.9 bc	2.9 bc	3.0 b	3.3 b	3.1 bc	2.9 bc	3.0 c	3.0 c
	91A	···	···	···	2.9 b	2.0 b	2.5 b	···	···	···	2.6 b	2.5 b	2.6 b
	105A	3.0 c	2.8 b	2.9 c	···	···	···	2.8 b	3.0 b	2.9 b	···	···	···
	S89-4	3.0 c	3.0 b	3.0 c	3.0 b	3.1 c	3.1 cd	3.5 c	3.3 b	3.4 c	3.1 c	3.1 c	3.1 c

[x]Manapal and Walter are susceptible to both races of *V. dahliae*; Flora-Dade and Monte Carlo are resistant to race 1 but susceptible to race 2.
[y]Symptom severity based on a scale of 0–5, where 0 = no symptoms, 1 = chlorosis and wilting of the cotyledons, 2 = chlorosis and wilting of first true leaf, 3 = symptoms on lower 50% of foliage, 4 = symptoms on 51–100% of foliage, and 5 = dead plant. Values for each cultivar represent a mean of four and eight replicates in 1978 and 1979, respectively. Avg. = mean for both cultivars.
[z]Values in each column followed by the same letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.

no disease (0%) and slight (0.5–10%), moderate (11–25%), and severe (26–100%) disease incidences were established. When individual fields were grouped into these disease incidence classes, 44, 25, 11, and 19% of the surveyed fields or 43.5, 27.1, 12.5, and 16.9% of the surveyed hectares had no disease and slight, moderate, and severe disease incidences, respectively. Disease incidence was moderate to severe on 29.4% of the surveyed hectares.

Isolate screening. All 96 isolates of *V. dahliae* produced typical Verticillium wilt symptoms on susceptible cultivars in greenhouse tests. Seven isolates (50A, 58A, 59B, 88A, 91A, 105A, and 107B) were also pathogenic on the race 1-resistant cultivars and were designated race 2 of *V. dahliae*. The remaining 89 isolates were designated race 1 of *V. dahliae*. All the race 2 isolates were recovered from race 1-susceptible tomato cultivars during the survey. Six of the race 2 isolates came from fields not previously cropped with race 1-resistant cultivars. One race 2 isolate (107B) was recovered from a plant of the susceptible cultivar Manapal in a field where race 1-resistant cultivar Monte Carlo had been grown the previous year. The seven race 2 isolates were found in seven of the 11 counties surveyed.

V. dahliae was reisolated from stem vascular tissue of all race 1-resistant plants previously inoculated with race 2 isolates and displaying typical wilt symptoms during the tests. The pathogen was also reisolated from several non-symptomatic, race 1-resistant plants previously inoculated with race 1 isolates.

Pathogenicity of race 1 and race 2 isolates in the greenhouse. The race 1 isolates (CF and 20B) produced moderate to severe symptoms (2.8–4.5, based on a scale of 0–5) on the susceptible cultivars but were not pathogenic on the race 1-resistant cultivars (Table 1). The race 2 isolates (50A, 91A, 105A, and S89-4) produced mild to moderate symptoms (2.0–3.5) on both susceptible and race 1-resistant cultivars. Wilting of susceptible cultivars inoculated with either race 1 or race 2 occurred well in advance of chlorosis and necrosis. Wilting on race 1-resistant cultivars inoculated with race 2 was confined to chlorotic areas on leaflets. Slight stunting was the only visible reaction of the race 1-resistant cultivars to inoculation with race 1. No symptoms were observed on plants dipped in pathogen-free agar slurry.

The California race 2 isolate (S89-4)

Table 2. Symptom severity, yield, and yield loss for susceptible (S) and resistant (R) tomato cultivars inoculated in the field with races 1 and 2 of *Verticillium dahliae*

Year	Cultivar	Isolate	Race	Symptom severity[a]	Yield[b] (t/ha)	Yield loss[c] (%)
1977	Manapal (S)	Control	···	3.0	138.6	···
		CF	1	5.6	86.4	37.6
		20A	1	6.3	85.8	38.1
		59B	2	4.6	128.2	7.5
		50A	2	4.1	132.1	4.7
		105A	2	5.1	135.4	2.3
	Walter (S)	Control	···	1.5	142.7	···
		CF	1	8.8	75.4	47.1
		20A	1	9.6	76.4	46.5
		59B	2	6.5	112.0	21.5
		50A	2	7.3	98.1	31.2
		105A	2	6.9	98.9	30.7
	Flora-Dade (R)	Control	···	0.0	160.8	···
		CF	1	1.0	157.6	2.0
		20A	1	0.0	155.1	3.5
		59B	2	4.3	131.6	18.2
		50A	2	6.0	131.4	18.2
		105A	2	6.0	129.7	19.3
	Monte Carlo (R)	Control	···	0.3	171.9	···
		CF	1	0.8	160.7	6.5
		20A	1	0.5	163.6	4.8
		59B	2	3.3	135.8	21.0
		50A	2	3.9	132.7	22.8
		105A	2	3.3	134.0	22.1
1978	Manapal (S)	Control	···	0.0	174.7	···
		CF	1	6.5	105.0	39.9
		20B	1	5.4	118.4	32.3
		50A	2	2.6	156.8	10.3
	Walter (S)	Control	···	0.0	141.0	···
		CF	1	7.4	81.7	42.1
		20B	1	6.8	94.7	32.8
		50A	2	3.3	112.6	20.1
	Flora-Dade (R)	Control	···	0.0	135.7	···
		CF	1	0.0	161.0	0.0
		20B	1	0.0	163.3	0.0
		50A	2	0.8	120.6	11.1
	Monte Carlo (R)	Control	···	0.0	188.9	···
		CF	1	0.0	199.6	0.0
		20B	1	0.0	198.8	0.0
		50A	2	0.5	172.5	8.7

[a]Symptom severity was estimated 79 days after transplanting and was based on a scale of 0–10, where 0 = no symptoms and 10 = dead plant or 100% of the foliage chlorotic and necrotic. Values are means of four replicates with four observations (plants) per replicate.
[b]Yield was recorded weekly for 9 and 10 wk in 1977 and 1978, respectively. Values are means of four replicates.
[c]Yield loss (%) = [1 − (treatment yield/control yield)] × 100.

behaved similarly to the North Carolina race 2 isolates (50A, 91A, and 105A) on both the susceptible and race 1-resistant cultivars (Table 1).

The race 1 isolates as a group were significantly more virulent (greater symptom severities) than the race 2 isolates on the susceptible cultivars (Table 1).

Pathogenicity of race 1 and race 2 isolates in the field. The race 1 and race 2 isolates produced moderate to severe foliar symptoms (4.1–9.6, based on a scale of 0–10) on the susceptible cultivars Manapal and Walter in 1977 (Table 2). In 1978, the race 1 isolates produced moderate to severe symptoms (5.4–7.4) on the susceptible cultivars, but the race 2 isolate produced only mild symptoms (2.6–3.3). The race 2 isolates produced moderate symptom severities (3.3–6.0) on the race 1-resistant cultivars in 1977 but only slight symptom severities in 1978. Based on foliar symptom severity, race 1 isolates were significantly more virulent than race 2 isolates on the susceptible cultivars, and race 2 isolates were significantly more virulent than race 1 isolates on the race 1-resistant cultivars (Tables 2 and 3).

Race 1 isolates reduced mean yields of Manapal, Walter, Flora-Dade, and Monte Carlo by as much as 39.9, 47.1, 3.5, and 6.5%, respectively (Table 2). Race 2 isolates reduced mean yields of Manapal, Walter, Flora-Dade, and Monte Carlo by as much as 10.3, 31.2, 19.3, and 22.8%, respectively. Race 1 isolates reduced yield of susceptible Manapal and Walter in 1977 and 1978 significantly more than race 2 isolates did (Tables 2 and 3). Race 2 isolates reduced yield of race 1-resistant Flora-Dade in 1977 and 1978 and Monte Carlo in 1977 significantly more than race 1 isolates did.

In 1977, Manapal and Walter were severely diseased (based on symptom severity) 42 days after transplanting to the field. By the end of the growing season (115 days after transplanting), indeterminate Manapal, but not determinate Walter, had recovered slightly from the damage incited earlier by the race 1 and race 2 isolates. Symptom severity and yield loss at the end of the season were greater on Walter than on Manapal for each pathogen isolate (Table 2).

Table 3. Analysis of variance for symptom severity and yield of susceptible and resistant tomato cultivars inoculated in the field with races 1 and 2 of *Verticillium dahliae* in 1977

			Mean square	
Cultivar	Source	df	Symptom severity	Yield (t/ha)
Manapal	Blocks	3	0.20	64.96
	Isolates	5	1.32**[a]	591.88**
	CK vs. others[b]	1	3.85**	505.12**
	R1 vs. R2[c]	1	2.07**	2,428.65**
	CF vs. 20A[d]	1	0.20	0.17
	59B vs 50A/105A[e]	1	0.00	20.26
	50A vs. 105A[f]	1	0.50*	5.20
	Error	15	0.11	21.74
Walter	Blocks	3	0.48	56.70
	Isolates	5	8.03**	605.55**
	CK vs. others	1	33.08**	2,057.58**
	R1 vs. R2	1	6.42**	851.73**
	CF vs. 20A	1	0.38	0.45
	59B vs. 50A/105A	1	0.21	117.71
	50A vs 105A	1	0.07	0.30
	Error	15	0.58	64.76
Flora-Dade	Blocks	3	0.14	59.80
	Isolates	5	8.29**	214.04*
	CK vs. others	1	9.92**	312.18*
	R1 vs. R2	1	29.01**	753.00**
	CF vs. 20A	1	0.50*	3.00
	59B vs 50A/105A	1	2.04**	0.68
	50A vs. 105A	1	0.00	1.32
	Error	15	0.08	60.87
Monte Carlo	Blocks	3	0.02	183.09
	Isolates	5	2.70**	296.57**
	CK vs. others	1	3.59**	565.50**
	R1 vs. R2	1	9.63**	908.88**
	CF vs 20A	1	0.03	3.99
	59B vs 50A/105A	1	0.07	3.76
	50A vs. 105A	1	0.20	0.72
	Error	15	0.32	57.98

[a] ** = Significant F-test ($P = 0.01$), * = significant F-test ($P = 0.05$).
[b] Contrast between the uninoculated control (CK) and the inoculated treatments (others).
[c] Contrast between the race 1 (R1) isolates (CF and 20A) and the race 2 (R2) isolates (50A, 59B, and 105A).
[d] Contrast between race 1 isolate CF and race 1 isolate 20A.
[e] Contrast between race 2 isolate 59B and the other race 2 isolates (50A and 105A).
[f] Contrast between race 2 isolate 50A and race 2 isolate 105A.

DISCUSSION

Verticillium wilt has become prevalent throughout the commercial tomato-producing region of western North Carolina. The frequent cropping of susceptible tomato cultivars, such as Manapal and Walter, along with burley tobacco, a reported alternate host (14), has resulted in severe occurrences of the disease in some fields throughout the region.

Seven isolates of *V. dahliae* produced wilt symptoms on plants of race 1-resistant cultivars. These seven isolates were designated race 2 solely on the basis of their pathogenicity (symptom development) on cultivars possessing the *Ve* gene for resistance to race 1 of *V. dahliae*, the criterion used by Grogan et al (9) for identifying tomato races of *V. dahliae*. The North Carolina race 2 isolates responded similarly to a California race 2 isolate on susceptible and race 1-resistant cultivars.

Although individual isolates of each race varied in virulence, the race 2 isolates, on the average, were less virulent than the race 1 isolates on susceptible cultivars. This agreed with the observations of other researchers (7,9). In the field tests, the race 2 isolates were more virulent (greater symptom severity ratings and yield losses) on the susceptible determinate cultivar Walter than on the race 1-resistant cultivars. Other researchers have likewise reported race 2 isolates were more virulent on susceptible cultivars than on race 1-resistant cultivars (1,9), but this was not true in our experiments for the susceptible indeterminate cultivar Manapal.

In the 1977 field tests, Manapal, but not Walter, had partially recovered by the end of the growing season from the damage incited earlier by race 1 and race 2 isolates. The lower yield losses caused by race 1 and race 2 isolates on Manapal may have been due to this recovery of the plants. Visser (22) observed a similar reaction for plants inoculated before transplanting to the field. It is possible that the inoculum applied to the seedlings infected only some of the roots. Uninfected roots could have grown through the small volume of infested soil surrounding the plant and into the uninfested soil beyond. Vascular tissue associated with the uninfected roots may have remained uncolonized by the pathogen and was adequate to support good plant growth and yield.

Manapal may have a resistance mechanism that imparts tolerance to infection by *V. dahliae*. In both field tests, Manapal had less yield loss than Walter. Manapal was grown in western North Carolina for 12–15 yr before the introduction of Walter, and Verticillium wilt was never considered a serious problem until after Walter was introduced

into the region (P. B. Shoemaker, *unpublished*). The tolerance or less severe reaction of Manapal to Verticillium wilt may be related to its continued growth throughout the growing season, ie, indeterminate growth, with the production of new roots and stem vascular tissue that may escape later colonization by the pathogen.

Race 2 isolates did not cause the extensive wilting of foliage on the race 1-resistant cultivars that they and the race 1 isolates caused on susceptible cultivars. Wilting on race 1-resistant cultivars inoculated with race 2 was limited to chlorotic areas on leaflets. Wilting on susceptible cultivars inoculated with race 1 or race 2 isolates occurred well up the plant in advance of chlorosis. This difference in wilting may be due to a different response of the race 1-resistant cultivars versus the susceptible cultivars to metabolites or toxins produced by race 2 isolates or race 1 and race 2 may produce different metabolites and toxins. The difference in wilting may explain, in part, why race 1 isolates reduced yields of susceptible cultivars by 30–69% in this study and in others (2,8,12) but race 2 isolates reduced yields of susceptible cultivars by only 2–31% and race 1-resistant cultivars by only 23–25% in this study and in others (9).

Race 2 pathotypes are a natural component of the *V. dahliae* population in western North Carolina. Race 2 was widely distributed in western North Carolina (seven of 11 counties surveyed) and was recovered from fields never cropped with tomato cultivars possessing the *Ve* gene for resistance to race 1. Since 1977, Flora-Dade had been used extensively in the region. As soon as 1979, Verticillium wilt symptoms were apparent on plants in about 50% of the fields growing race 1-resistant cultivars (P. B. Shoemaker, *unpublished*). Race 2 pathotypes could have arisen as a mutation from tomato race 1 isolates (17) or evolved from *V. dahliae* isolates pathogenic on other hosts (7,16,18,21).

Race 1 in California is still prevalent despite extensive use of race 1-resistant tomato cultivars for the past 20 yr (9). The continued prominence of race 1 may be due to slow decline of ms numbers in soil (11), infection of weed hosts and other host crops (14), and infection of race 1-resistant tomato cultivars (6,9). Although *V. dahliae* was recovered from stems of race 1-resistant cultivars inoculated with race 1 isolates in this study, survival of race 1 isolates by colonization of race 1-resistant cultivars depends on successful production of ms as overwintering inoculum in the stems and roots of race 1-resistant cultivars.

Economic losses on susceptible Manapal and Walter were occurring in some fields in western North Carolina in 1974 and 1975 and were fairly extensive by 1976 (P. B. Shoemaker, *unpublished*). This has necessitated the change by growers to race 1-resistant cultivars, principally, Flora-Dade. As the use of tomato cultivars with the *Ve* gene for resistance to race 1 continues, the prevalence of race 2 will probably increase and serious yield losses as high as 25% may occur. Development of new tomato cultivars resistant to both race 1 and race 2 is needed. Unfortunately, no source of high level resistance to race 2 has been found (10,15), but a source of moderate level resistance to race 2 has been identified and is being evaluated for use in breeding tomato cultivars adapted to western North Carolina (15).

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