Inoculation with *Fusarium* and *Verticillium* to Increase Resistance in *Fusarium*-Resistant Tomato

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ABSTRACT

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Increased resistance to Verticillium wilt was confirmed in *Fusarium*-resistant tomato (*Lycopersicon esculentum*) cultivars when plants were root-dip inoculated simultaneously with *Fusarium oxysporum* f. sp. *lycopersici* (inducer) and *Verticillium dahliae* (challenger). The level of resistance diminished progressively as the time interval between inducer and challenger inoculations was increased and also as the concentration of the inducer inoculum was reduced in relation to the challenger inoculum. Increased resistance also occurred at lower but significant levels in a *Verticillium*-resistant tomato cultivar when *V. dahliae* was the inducer and *F. o. lycopersici* the challenger organism. Increased resistance in both cases appears attributable to either pathogen antagonism at the root surface or a localized, rather than a systemically induced, host response.

Induced resistance involving vascular wilt pathogens, specifically *Verticillium* spp. and *Fusarium* spp., has been reported in a wide range of hosts (2,4–6,9). Schnathorst and Mathre (6) observed protection of cotton (*Gossypium hirsutum* L.) against a severe strain of *V. albo-atrum* Reinke & Berthier induced by a mild strain of the same fungus. Melouk and Horner (4) reported protection of peppermint (*Mentha* × *piperita* L.) and spearmint (*M. cardiaca* (S. F. Gray) Baker) induced by *V. nigrescens* Pethybr. against subsequent challenge inoculations with *V. dahliae* Kleb. The induction of resistance in cotton plants by a nonpathogenic strain of *F. oxysporum* Schlechtend.:Fr. f. sp. *vasinfectum* (Atk.) W. C. Snyder & H. N. Hans. against a pathogenic strain of the fungus was reported by Hillocks (2). Wymore and Baker (9) observed that seedlings of the tomato (*Lycopersicon esculentum* Mill.) cultivar Bonny Best showed a reduction of symptoms when previously inoculated with *F. o.* f. sp. *dianthi* (Prill. & Delacr.) W. C. Snyder & H. N. Hans. and challenged with *F. o.* f. sp. *lycopersici* (Sacc.) W. C. Snyder & H. N. Hans. Ogawa and Komada (5) reported induced resistance in sweet potato using a nonpathogenic *F. oxysporum* against the pathogen *F. o.* f. sp. *batatas* (Wollenweb.) W. C. Snyder & H. N. Hans. in greenhouse and field studies. For all the above reports, an interval of time was needed between inducer and challenger inoculations for the expression of resistance.

Tigchelaar and Dick (7) found that when tomato seedlings were screened simultaneously for resistance to the vascular pathogens *V. dahliae* and *F. o. lycopersici*, progenies resistant to *F. o. lycopersici* also exhibited resistance to *V. dahliae* even though these progenies were genetically susceptible to the latter pathogen. They also suggested that the reciprocal type of induced resistance, i.e., progeny resistant to *V. dahliae* but susceptible to *F. o. lycopersici*, did not occur. This study was based primarily on symptom responses, namely vascular discoloration. Inoculum preparation and environmental parameters were not controlled.

Our objective was to attempt to confirm induced resistance to *V. dahliae* in *Fusarium*-resistant tomato cultivars with more precise control of inoculum preparation and environmental conditions. The effects of simultaneous inoculation, inoculum concentration, and time intervals between inducer and challenger inoculations on qualitative and quantitative expressions of increased resistance were studied.

MATERIALS AND METHODS

Source of isolates. Isolates of *F. o. lycopersici* and *V. dahliae*, virulent to tomato, were provided by J. F. Tuite, Department of Botany and Plant Pathology, Purdue University, West Lafayette, IN, and J. C. Watterson, Petoseed Research Center, Woodland, CA, respectively.

Preparation of inoculum. *F. o. lycopersici* cultures from potato-dextrose agar (PDA) slants were blended aseptically with sterile deionized water. A mycelium spore suspension (5 ml) was transferred to Erlenmeyer flasks containing Tochinai nutrient solution (8) and incubated on a shaker under fluorescent lights at 26 C for 4 days. Cultures were filtered through several thicknesses of cheesecloth and washed twice by centrifugation at 4,000 rpm (centrifugal force = 1935 *g*) for 15 min, followed by resuspension of the pellet containing conidia in 0.1% water agar (WA) to assure uniform inoculum suspension. *V. dahliae* cultures from PDA slants were blended as above, and 3 ml was pipetted and spread evenly over PDA plates (150 × 20 mm). Cultures were incubated for 6–8 days, flooded with 0.1% WA, scraped gently to free the conidia, and filtered through cheesecloth. The final suspension consisted primarily of conidia and some chlamydospore-like cells. The stock spore concentration was determined with a hemacytometer. The final spore concentrations were prepared for both organisms by appropriate dilutions of the stock spore suspensions.

Inoculation and incubation procedures. Tomato plants were grown from seed in trays of washed river sand (pH 6.0–7.0) in a greenhouse. Seedlings were fertilized (10-52-8 N-P-K) once in the second-true-leaf stage. Seedlings in the fourth-true-leaf stage were lifted, and roots were washed carefully in tap water, blotted on paper toweling, and inoculated by dipping roots for 2 min into the spore suspensions. Four seedlings were planted in each double cylindrical plastic container (15 × 19 cm) containing a sterile mixture of soil/peat/sand (3:1:1, v/v/v). The inner plastic container had drainage holes in the bottom. After planting and fertilization, the containers were arranged in temperature-controlled water tanks at 22 ± 1 C. Supplemental light was provided for 15 hr by banks of four fluorescent lamps. However, ambient temperatures were not controlled and ranged from 28 to 32 C during the day and from 25 to 28 C at night. Experiments were terminated when the susceptible check plants exhibited severe disease symptoms.

Disease evaluation. A symptom severity rating scale based on characteristic shoot symptoms, i.e., leaf chlorosis, leaf necrosis, defoliation, stunting, wilting,

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and shoot necrosis, was used. This scale ranged from 0 (no symptoms) to 5 (severe symptoms). Vascular discoloration proved to be an unreliable symptom and was not included (3). To determine fresh weight, stems were cut at the soil line and weighed immediately.

Stem colonization. Surface-disinfested stem sections, approximately 2 cm long, from basal, middle, and apical areas of the stem were plated on PDA amended with the surfactant Tergitol (100 ppm) and chlortetracycline (Aureomycin) (30 ppm) (PDTA) (8) to determine stem colonization by *F. o. lycopersici* and/or *V. dahliae*. Characteristic colonies of either fungus were recorded as present or absent for the specific stem section after 10–12 days of incubation at room temperature.

Increased resistance studies. *Simultaneous inoculation.* The Gardner V (resistant to *V. dahliae* and susceptible to *F. o. lycopersici*) and Roma F (resistant to *F. o. lycopersici* and susceptible to *V. dahliae*) tomato cultivars were inoculated simultaneously by root dip in a conidial suspension of one or both pathogens at concentrations of 7×10^6 propagules per milliliter of 0.1% WA. Separate experiments were established for each cultivar. The following four treatments were imposed: 1) induced/challenged—inoculum containing equal spore concentrations of each fungus; 2) induced/nonchallenged—inoculated only with *V. dahliae* (Gardner V) or only with *F. o. lycopersici* (Roma F); 3) noninduced/challenged—inoculated only with *F. o. lycopersici* (Gardner V) or only with *V. dahliae* (Roma F); and 4) noninduced/nonchallenged (control)—root dipped in 0.1% WA. Treatments were arranged in a randomized complete block design with five replications and incubated for 21–23 days (Gardner V) and 31–33 days (Roma F) at a controlled soil temperature of 22 ± 1 C and ambient air temperature.

Effect of inoculum concentration. The effect of varying the concentration of *F. o. lycopersici* inoculum (inducer) on the increased level of resistance in the tomato cultivar Kokomo F (resistant to *F. o. lycopersici* and susceptible to *V. dahliae*) against *V. dahliae* (challenger) was tested. Treatments included a mixed inoculum of the two fungi with a constant concentration of *V. dahliae* of 7×10^6 propagules per milliliter and concentrations of *F. o. lycopersici* of 7×10^6, 7×10^5, or 7×10^3 propagules per milliliter, as well as treatments in which seedlings were only induced (*F. o. lycopersici*), only challenged (*V. dahliae*), or noninduced/nonchallenged (control). Treatments were arranged in a randomized incomplete block design with six replications. After treatment, plants were grown for 23 days at a soil temperature of 22 ± 1 C and ambient air temperature.

Effect of time interval. Seedlings of the cultivar Roma F were root-dip inoculated with a conidial suspension of *F. o. lycopersici* (7×10^6 conidia per milliliter of 0.1% WA), planted temporarily in sand, and then lifted to be challenge-inoculated with *V. dahliae* (7×10^6 propagules per milliliter of 0.1% WA) at 3-day intervals for up to 12 days. Treatments were arranged in a randomized complete block design with four replications and grown for 32 days at soil temperature of 22 ± 1 C and ambient air temperature.

Statistical analysis. Data were analyzed using the Statistical Analysis System (SAS Institute, Inc., Cary, NC). Analysis of variance and Duncan's multiple range test at the 5% level were applied to the fresh weight and symptom severity ratings. Chi-square tests at the 5% level were applied to the isolation of the fungi from stem sections.

RESULTS

Simultaneous inoculation. *Gardner V.* The level of resistance to *F. o. lycopersici* increased in the *Verticillium*-resistant cultivar Gardner V when inoculated simultaneously with *V. dahliae* and *F. o. lycopersici* (Table 1). The *F. o. lycopersici* and *V. dahliae* + *F. o. lycopersici* treatments had significantly lower fresh weights than the *V. dahliae* and control treatments. The *V. dahliae* + *F. o. lycopersici* inoculated treatment showed a significantly higher fresh weight and lower symptom ratings than the *F. o. lycopersici* treatment. The frequency of isolation of the two pathogens from stem sections showed no significant differences between treatments. *Fusarium* was isolated from 98% of the total stem sections of the *F. o. lycopersici* treatment and from 75% of the sections of the *V. dahliae* + *F. o. lycopersici* treatment. *Verticillium* was not isolated from the *V. dahliae* treatment, but it was isolated from 20% of the sections from plants treated with *V. dahliae* + *F. o. lycopersici*.

Roma F. The level of resistance to *V. dahliae* also increased in the *Fusarium*-resistant cultivar Roma F when inocu-

Table 1. Fresh weights and symptom ratings for the tomato cultivars Gardner V[v] and Roma F[w] inoculated separately and simultaneously with *Fusarium oxysporum* f. sp. *lycopersici* and *Verticillium dahliae*

Treatment	Gardner V		Roma F	
	Fresh weight (g)[x]	Symptom rating[y]	Fresh weight (g)	Symptom rating
Control	73.3 a[z]	0.0	87.4 a	0.0
F. o. lycopersici	6.9 b	4.9 a	85.7 a	0.0
V. dahliae	74.3 a	0.0	30.0 b	3.7 a
V. dahliae + *F. o. lycopersici*	15.8 c	3.1 b	83.6 a	0.3 b

[v] Gardner V is resistant to *V. dahliae* and susceptible to *F. o. lycopersici*. Inoculated plants were incubated for 21 days.
[w] Roma F is resistant to *F. o. lycopersici* and susceptible to *V. dahliae*. Inoculated plants were incubated for 31 days.
[x] Mean shoot fresh weight based on five repetitions and four plants per repetition.
[y] Mean symptom severity ratings from 0 to 5 (0 = healthy, 5 = severe).
[z] Means in the same column with different letters differ statistically at the 5% level using Duncan's multiple range test.

Table 2. Isolation of *Verticillium dahliae* and/or *Fusarium oxysporum* f. sp. *lycopersici* from basal, mid, and apical stem sections of tomato cultivar Roma F[x] 31 days after inoculation

Treatment	No. of plants	Isolation frequency by stem section[y]					
		Base		Middle		Apex	
		V. dahliae	*F. o. lycopersici*	*V. dahliae*	*F. o. lycopersici*	*V. dahliae*	*F. o. lycopersici*
Control	20	0[z]	0	0	0	0	0
F. o. lycopersici	20	0	16	0	1	0	0
V. dahliae	20	20	0	20	0	10	0
V. dahliae + *F. o. lycopersici*	20	2	18	2	2	2	0

[x] Roma F is resistant to *F. o. lycopersici* and susceptible to *V. dahliae*.
[y] Stem sections were incubated for 10 days on PDTA medium.
[z] Observed values did not differ significantly from expected values at the 5% level using chi-square tests.

lated simultaneously with *V. dahliae* and *F. o. lycopersici* (Table 1). No significant differences were observed in mean fresh weights among the control, *F. o. lycopersici*, and *V. dahliae* + *F. o. lycopersici* treatments, whereas fresh weight was significantly lower in the *V. dahliae* treatment than the other three treatments. Significantly greater disease severity was observed in the *V. dahliae* than the *V. dahliae* + *F. o. lycopersici* treatment. In the *V. dahliae* treatment, 75% of the plants had symptom ratings of 4 and 5, whereas in the *V. dahliae* + *F. o. lycopersici* treatment, 90% of the plants were symptomless (20 plants per treatment).

V. dahliae was isolated from 83% of the stem sections from the *V. dahliae* treatment in contrast to 10% from the *V. dahliae* + *F. o. lycopersici* treatment (Table 2). *Fusarium* was isolated from 80 and 90% of the basal stem sections from the *F. o. lycopersici* and *V. dahliae* + *F. o. lycopersici* treatments, respectively. However, these were not statistically different using the chi-square test.

Effect of inoculum concentration. The increase in the level of resistance to Verticillium wilt in Kokomo F tomato plants decreased as the inoculum concentration of the inducer organism (*F. o. lycopersici*) decreased in comparison with the concentration of the challenger (*V. dahliae*) (Tables 3 and 4). The fresh weight of the control, *F. o. lycopersici* alone (7×10^6 propagules per milliliter), and *V. dahliae* + *F. o. lycopersici* at concentrations of 7×10^6 propagules per milliliter of 0.1% WA were not significantly different (Table 3). These three treatments had significantly greater fresh weights than the treatments including *V. dahliae* alone, *V. dahliae* + *F. o. lycopersici* at concentrations of 7×10^6 and 7×10^3 propagules per milliliter, and *V. dahliae* + *F. o. lycopersici* at concentrations of 7×10^6 and 7×10^5 propagules per milliliter. There were no differences in fresh weights among other treatments.

Mean symptom ratings for all treatments that included both *V. dahliae* and *F. o. lycopersici* inoculum were significantly lower than the treatment with *V. dahliae* alone, regardless of the inoculum concentration of *F. o. lycopersici* (Table 3). Symptom ratings were significantly different among the three treatments in which *V. dahliae* inoculum was constant at 7×10^6 propagules per milliliter as *F. o. lycopersici* varied from 7×10^3 to 7×10^5 and 7×10^6.

In the treatment with *V. dahliae* and *F. o. lycopersici* at 7×10^6, 60% of the plants were symptomless (20 plants per treatment), whereas 25% of the plants in the treatment with *V. dahliae* at 7×10^6 and *F. o. lycopersici* at 7×10^5 were symptomless. The treatments with *V. dahliae* at 7×10^6 and *F. o. lycopersici* at 7×10^3 and *V. dahliae* at 7×10^6 had 55 and 95% of the plants, respectively, with symptom ratings of 3 and 4.

The frequency of isolation of *V. dahliae* from stem sections increased as the concentration of *F. o. lycopersici* inoculum decreased (Table 4). *V. dahliae* was isolated from 40% of the stem sections of the treatment with *V. dahliae* and *F. o. lycopersici* at 7×10^6, in contrast to 62, 80, and 87% of the isolations from the treatments with *V. dahliae* at 7×10^6 and *F. o. lycopersici* at 7×10^5, *V. dahliae* at 7×10^6 and *F. o. lycopersici* at 7×10^3, and *V. dahliae* at 7×10^6, respectively. However, no statistical difference was observed.

Effect of time interval. The increase in the level of resistance in the Roma F cultivar to *V. dahliae* decreased or was lost when the time between inoculations with *F. o. lycopersici* (inducer) and *V. dahliae* (challenger) was increased from 3 to 12 days (Table 5). Plants inoculated simultaneously (*F. o. lycopersici* + *V. dahliae*) showed a significantly greater fresh weight and lower mean symptom severity rating than the plants that were not simultaneously inoculated (Table 5). Fresh weights and symptom ratings of the 6-, 9-, and 12-day interval challenge inoculations with *V. dahliae* did not differ significantly, whereas the 3-day interval treatment resulted in plants with intermediate fresh weight and symptom ratings.

At harvest, 63% of the plants simultaneously inoculated were symptomless, whereas 88% of plants challenge-inoculated 3 days later had symptom ratings between 0 and 3. In contrast, the 6-, 9- and 12-day interval challenge inoculation treatments had more than 93% of the plants with ratings between 3 and 5.

The frequency of isolation of *V. dahliae* and/or *F. o. lycopersici* from stems of tomato cultivar Roma F inoculated simultaneously or at varying time intervals is shown in Table 6. *V. dahliae* was isolated from 35% of stem sections from the plants simultaneously inoculated with both fungi (*F. o. lycopersici* + *V. dahliae*) compared with 69, 92, 100, and 94% isolation frequency from the stem sections of plants in the 3-, 6-, 9-, and 12-day interval challenge inoculation

Table 3. Effect of inoculum concentration of *Fusarium oxysporum* f. sp. *lycopersici* on the level of resistance to *Verticillium dahliae* in the tomato cultivar Kokomo F[w]

Inoculum concentration (propagules/ml)		Fresh weight (g)[x]	Symptom rating[y]
V. dahliae	*F. o. lycopersici*		
0	0	56.0 a[z]	0.0
0	7×10^6	58.8 a	0.0
7×10^6	0	27.1 b	3.4 a
7×10^6	7×10^3	28.8 b	2.5 b
7×10^6	7×10^5	32.0 b	1.9 c
7×10^6	7×10^6	50.5 a	0.7 d

[w] Kokomo F is resistant to *F. o. lycopersici* and susceptible to *V. dahliae*. Inoculated plants were incubated for 23 days.
[x] Mean shoot fresh weight based on five repetitions and four plants per repetition.
[y] Mean symptom severity ratings from 0 to 5 (0 = healthy, 5 = severe).
[z] Means in the same column with different letters differ statistically at the 5% level using Duncan's multiple range test.

Table 4. Effect of inoculum concentration of *Fusarium oxysporum* f. sp. *lycopersici* on the isolation of *Verticillium dahliae* and/or *F. o. lycopersici* from basal, mid, or apical stem sections of the tomato cultivar Kokomo F[x]

Inoculum concentration (propagules/ml)		No. of plants	Isolation frequency by stem section[y]					
			Base		Middle		Apex	
V. dahliae	*F. o. lycopersici*		*V. dahliae*	*F. o. lycopersici*	*V. dahliae*	*F. o. lycopersici*	*V. dahliae*	*F. o. lycopersici*
0	0	20	0[z]	0	0	0	0	0
0	7×10^6	20	0	0	0	0	0	0
7×10^6	0	20	19	0	18	0	15	0
7×10^6	7×10^3	20	17	0	17	0	14	0
7×10^6	7×10^5	20	12	0	13	0	12	0
7×10^6	7×10^6	20	8	0	9	0	7	0

[x] Kokomo F is resistant to *F. o. lycopersici* and susceptible to *V. dahliae*.
[y] Stem sections were incubated for 10 days on PDTA medium.
[z] Observed values did not differ significantly from expected values at the 5% level using chi-square tests.

treatments, respectively (Table 6). However, no statistically significant differences were observed.

DISCUSSION

Increased resistance to Verticillium wilt disease in tomato cultivars resistant to *F. o. lycopersici* but susceptible to *V. dahliae* was confirmed when plants were simultaneously inoculated with the two pathogens. A lower but statistically significant level of increased resistance to Fusarium wilt disease also was demonstrated with a tomato cultivar resistant to *V. dahliae* but susceptible to *F. o. lycopersici*. This is contrary to results reported by Tigchelaar and Dick (7). Our results are in agreement with those of Tigchelaar and Dick (7), Davis (1), and Wymore and Baker (9) in that the concentration of inoculum of the inducer organism must be equal to or greater than that of the challenger organism to attain the highest increase in resistance.

In this study, increases in resistance were greatest when plants were inoculated simultaneously with the two organisms. If inoculations were separated in time, increases in the level of resistance were reduced or lost. This is in contrast to reports of host-induced interactions with *Fusarium* spp. or *Verticillium* spp. by other investigators (1,6,9), who, in all instances, found that plants had to be induced or inoculated up to several days before challenge inoculations if resistance was to be expressed. Our results suggest that the increased resistance observed may be attributable to pathogen interactions or antagonisms at the root surface or a localized rather than systemically induced host response. The loss of resistance may be correlated with the initiation of new root growth, which was observed at the 3-day interval and beyond in the sequential inoculation studies (Table 5). The results suggest that the new root growth was unprotected and readily colonized by the challenge organism.

The increase in resistance demonstrated is important if progenies are screened simultaneously for genetic resistance to both pathogens. Plant breeders and others should be aware of the occurrence of this phenomenon as they select progenies apparently resistant to both pathogens.

Table 5. Effect of nonsimultaneous inoculation with *Fusarium oxysporum* f. sp. *lycopersici* and *Verticillium dahliae* on the level of resistance in the tomato cultivar Roma F[w]

Inoculation interval (days)		Fresh weight (g)[x]	Symptom rating[y]
F. o. lycopersici	*V. dahliae*		
0	0	90.3 a[z]	0.8 a
0	3	64.7 b	1.8 b
0	6	30.1 c	3.6 c
0	9	13.4 c	3.8 c
0	12	20.8 c	3.3 c

[w] Roma F is resistant to *F. o. lycopersici* and susceptible to *V. dahliae*. Inoculated plants were incubated for 32 days.
[x] Mean shoot fresh weight based on four repetitions and four plants per repetition.
[y] Mean symptom severity ratings from 0 to 5 (0 = healthy, 5 = severe).
[z] Means in the same column with different letters differ statistically at the 5% level using Duncan's multiple range test.

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Table 6. Effect of nonsimultaneous inoculation on the isolation of *Verticillium dahliae* and/or *Fusarium oxysporum* f. sp. *lycopersici* from basal, mid, or apical stem sections of the tomato cultivar Roma F[x]

Inoculation interval (days)		No. of plants	Isolation frequency by stem section[y]					
			Base		Middle		Apex	
F. o. lycopersici	*V. dahliae*		*F. o. lycopersici*	*V. dahliae*	*F. o. lycopersici*	*V. dahliae*	*F. o. lycopersici*	*V. dahliae*
0	0	16	8[z]	6	1	6	0	5
0	3	16	6	10	1	15	0	8
0	6	16	1	15	0	15	0	14
0	9	15	0	15	0	15	0	15
0	12	16	5	16	0	16	0	13

[x] Roma F is resistant to *F. o. lycopersici* and susceptible to *V. dahliae*.
[y] Stem sections were incubated for 10 days on PDTA medium.
[z] Observed values did not differ significantly from expected values at the 5% level using chi-square tests.