A Comparison of Resistance to *Phytophthora parasitica* in Tomato

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ABSTRACT

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The basis of resistance in tomato to *Phytophthora parasitica* was examined using three resistant genotypes, CX8303, 27-1A, and LA1312 and two susceptible cultivars, 6203 and Peto 343. Seedlings were grown hydroponically and inoculated with 2×10^6 zoospores. Microscopic examination of root tips 5 hr after inoculation showed no genotypic differences in the number of zoospores encysted on 2 cm of root tip. Linear colonization of taproots of young seedlings was examined by growing plants in root boxes and inoculating root tips with approximately 200 zoospores. After 3 days, roots were sectioned into 1-cm lengths, which were plated sequentially on $P_{10}VP$ medium. In 27-1A and LA1312, *P. parasitica* was only isolated < 2.5 cm from the root tip, whereas the fungus was detected 5.5–6.1 cm from the point of inoculation in the other three genotypes. The number of propagules of *P. parasitica* per gram of root tissue (ppg) in inoculated root systems was estimated by using root maceration and dilution plating methods. LA1312 and 27-1A had the lowest level of infection (2.1 and 3.2×10^3 ppg, respectively). CX8303 had significantly less infection (6.8×10^3 ppg) than Peto 343 and 6203 (14.1 and 9.7×10^3 ppg, respectively). Root growth after inoculation, or mechanical pruning in the absence of *P. parasitica*, was measured in three genotypes by using a grid intersect method. Four weeks after inoculation, total root lengths in 27-1A, CX8303, and Peto 343 were 1,714, 1,314, and 427 cm, respectively. There were no genotypic differences in total root length 2 wk after root pruning. All three genotypes had root lengths of 830–910 cm. Differences in root growth after inoculation may be due to differences in severity of root infection.

Additional key words: *Lycopersicon esculentum*, *Lycopersicon esculentum* var. *cerasiforme*.

Phytophthora root and crown rot, caused primarily by *Phytophthora parasitica* Dastur and *P. capsici* Leonian, is annually responsible for major losses in California processing tomatoes (3,10,18). Control strategies have generally focused on good water management and, to a lesser degree, use of chemicals. Recently, however, rapid and reliable methods for screening large numbers of tomato seedlings for resistance to *P. parasitica* were developed (3,19), and resistance was detected in both tomato cultivars and accessions of *Lycopersicon esculentum* var. *cerasiforme* (Dun.) A. Gray (2,3). Thus far, resistance has been identified in several tomato genotypes from diverse genetic backgrounds (2,3). A knowledge of the biological basis of resistance in tomato may be useful in designing a breeding program and in improving screening methods for resistance to *P. parasitica*.

The purpose of this study was to determine quantitatively the basis of resistance in one commercial tomato cultivar and two accessions of *L. esculentum* var. *cerasiforme*.

MATERIALS AND METHODS

Three tomato cultivars, Peto 343, 6203, and CX8303 obtained from seed companies and two accessions of *L. esculentum* var. *cerasiforme*, LA1312 and 27-1A, collected by C. M. Rick (Department of Vegetable Crops, University of California, Davis) were grown from seed in a steam-pasteurized UC mix (14) in all experiments. In previous studies (2,3), Peto 343 and 6203 were found to be susceptible to *P. parasitica*, whereas CX8303, LA1312, and 27-1A were determined to be equally resistant. A pathogenic isolate of *P. parasitica* (obtained from R. G. Grogan, University of California, Davis) was used to inoculate tomato lines. Zoospore inoculum was prepared by growing *P. parasitica* on V-8 agar plates at 24 C for 7 days. Colonized agar plates were cut into approximately 4-cm pieces, and contents of five plates were placed in a 30- × 23-cm plastic box containing 300 ml of 2% aqueous soil extract and incubated at 24 C for 48 hr to obtain numerous sporangia. Sporangia were induced to release zoospores by chilling at 4 C for 20 min, followed by rewarming at 25 C. Zoospores were separated from agar by filtration through a single layer of cheesecloth.

Zoospore encystment. Six seedlings of each genotype were removed from the UC mix, established in a hydroponic system, and inoculated as described by MacDonald (13). Plants were grown in 2-L ceramic crocks to the three-leaf stage, at which time seedlings were removed from the crocks and placed in beakers containing 2×10^6 motile zoospores in 400 ml of distilled water for 5 hr. To minimize the possibility of wounding, roots were not directly handled during the inoculation procedure. Twenty 2-cm-long root tips were clipped from each genotype and fixed in 2% glutaraldehyde in 0.1 M phosphate buffer (pH 7.2). Root tips were mounted on glass slides, stained with acid fuchsin in lactophenol, and viewed at ×100 magnification to count the number of encysted zoospores on each root (13). This experiment was repeated twice, and data were analyzed by using a one-way analysis of variance.

Root colonization. Root colonization was studied in two ways. The extent of linear hyphal growth from infected root tips and severity of infection based on the number of fungal propagules in the entire root system were both examined.

To determine the distance *P. parasitica* could colonize from a single infection site, seedlings were grown in thin, modified root boxes (20 × 30 × 2 cm) made from the lids of plastic boxes. The front faces of the root boxes were made from clear 0.5-cm-thick acrylic to allow undisturbed access to roots. A clear acetate sheet was placed between the soil and the acrylic face to prevent roots from adhering to the acrylic. The root boxes were held together by two clips on each side and were covered with aluminum foil to block light. Fifteen seeds of each genotype were planted at the top of the root box between the soil and acetate sheet. Root boxes were placed upright in a growth chamber adjusted to provide 16-hr of light with 28 C day and 26 C night temperatures. Seedlings were watered twice daily with distilled water.

Ten to fourteen days after planting, taproots of 10 seedlings in each root box were inoculated by removing the acrylic face and acetate sheet and placing a holder made from a 2-cm-long piece of tygon tubing cut in half longitudinally under the root tip. A 20-μl drop containing an average of 200 zoospores was placed on each root tip. The acetate sheet was replaced over roots and soil and covered with moist paper towels to prevent the roots from drying.

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After 2 hr, holders were removed, and six 0.5-cm leaf disks cut from newly emerged citrus leaves were placed along the length of the taproot, 2 to 3 mm away from the root as bait, to detect any secondary zoospore production. Previous experiments had shown that the isolate of *P. parasitica* used in these experiments would readily infect citrus leaves at a concentration of < 20 zoospores per milliliter. Boxes were reassembled and returned to the growth chamber.

Three days after inoculation, lateral roots were clipped off, and adhering soil was rinsed with distilled water from the taproots. Roots were sectioned into 1-cm segments and arranged on $P_{10}VP$ (16) agar plates sequentially according to distance from the root tip. After 3 days at 25 C, the extent of root colonization was assessed by counting the number of consecutive segments from which mycelium of *P. parasitica* could be observed growing in the medium. Citrus leaf disks also were plated out on $P_{10}VP$ medium to detect the presence of *Phytophthora*. Root colonization experiments were repeated twice, and data from both experiments were combined and analyzed using a one-way analysis of variance.

The rate of linear colonization was studied over 4 days in Peto 343, CX8303, and 27-1A. Seedlings were grown and inoculated as described above. At 24-hr intervals after inoculation, 7–10 taproots from seedings of each genotype were removed from the root boxes, sectioned, and plated out as before. Because of the difficulty in uniformly inoculating large numbers of roots and a limited number of root boxes, all seedlings in the study could not be inoculated simultaneously; however, all seedlings within a given time interval were inoculated at the same time. Experiments at each 24-hr interval were repeated three times, and data were combined.

The severity of root infection was determined by estimating the number of propagules of *Phytophthora* per gram of root tissue by using root maceration and dilution plating techniques similar to those of Kellam and Coffey (11). Sixteen seedlings of each genotype were transplanted into 10-cm-diameter pots (four plants per pot) containing steam-pasteurized river sand and irrigated daily with water or nutrient solution (Plantex, 15N-15P-30K, Plantco, Inc., Bramalea, Ontario, Canada) on alternate days. Plants were grown in the greenhouse for 4 wk, at which time they were inoculated by adding 15 ml of soil extract containing 10^6 zoospores to each pot and were then flooded with distilled water for 24 hr. To prevent secondary inoculum production, plants were not irrigated after the flooding period and showed no symptoms of drought stress (1). Three days after inoculation, tops of plants were cut at soil level and discarded. All roots were removed from pots, rinsed free of adhering sand, and uniformly blotted between eight layers of paper towel. Roots from each pot were weighed and ground in 30 ml of distilled water in a Waring blender at high speed for 2 min. The macerated suspension was diluted 1:10 and 1:50 with distilled water, and 1-ml samples of each dilution were spread on each of five replicate plates of $P_{10}VP$ medium. Colonies were counted after 2 and 3 days, and the propagules of *Phytophthora* per gram fresh weight of roots were calculated. This experiment was repeated three times and was analyzed using Duncan's multiple range test.

Root growth. Root growth after inoculation was studied over a 4-wk period in 27-1A, CX8303, and Peto 343. Seeds were sown in 45 10-cm-diameter pots per genotype and maintained under greenhouse conditions. On emergence, seedlings were thinned to one plant per pot. At early flowering, 20 plants of each line were inoculated with 10^6 zoospores per plant and flooded for 24 hr as described above, and 20 plants were flooded only and served as uninoculated controls. Roots of the remaining five plants were harvested before inoculation for an initial root measurement. Root systems of five plants of both inoculated and uninoculated plants were destructively harvested every 7 days after inoculation for root length measurements. Root systems were rinsed free of UC mix, cut into pieces, and randomly spread between two 21- × 29-cm sheets of glass on which a grid had been drawn. The distance between grid lines was 1.25 cm. Root length for each plant was estimated using a grid intersect method described by Tennant (4,22). Root growth experiments were repeated twice and analyzed at week 4 using Duncan's multiple range test.

Potential root regeneration of uninoculated plants also was compared in the same tomato lines. Plants of each genotype were grown as described above. At flowering, five plants of similar size were unpotted and all roots were clipped 5 cm from the crown. Plants were then repotted and grown for 2 wk at which time total root length per plant was measured as described above. Potential root growth experiments were repeated twice and analyzed using a one-way analysis of variance.

RESULTS

Zoospore encystment. When zoospore encystment was compared on roots of resistant and susceptible lines, there was a high degree of variability among roots from the same plant and genotype. Within any genotype, the number of zoospore cysts on a 2-cm root tip ranged from two to nearly 100, and there were no significant differences in zoospore encystment between tomato lines. All genotypes had an average of 14–29 zoospore cysts per root tip (Table 1).

Root colonization. Differences in the linear extent of root colonization from a single point of inoculation were apparent between resistant and susceptible genotypes. In both *cerasiforme* accessions, LA1312 and 27-1A, *P. parasitica* was isolated only within 2.5 cm of the inoculated root tip 3 days after inoculation. The fungus was detected approximately 6 cm from the root tip in the other three cultivars (Table 1). The total root length of inoculated roots ranged from 9 to 17 cm. *Phytophthora* was not isolated from citrus leaf bait that were placed alongside inoculated roots. Therefore, we believe that the presence of *P. parasitica* in root tissue above the root tip was due to fungal growth through the root and not infection by secondary inoculum.

When the linear colonization of roots was examined at 24-hr intervals after inoculation, significant differences between genotypes were observed within 48 hr (Fig. 1). The rate of colonization in 27-1A was significantly slower over the 96-hr period than in Peto 343 and CX8303. Within genotypes, there were no detectable increases in root colonization between 72 and 96 hr. It is not clear if fungal growth within roots was arrested or simply slowed after 72 hr, and colonization studies beyond 96 hr are not feasible in these root boxes.

When the relative intensity of root infection was studied using a

TABLE 1. Comparison of zoospore encystment, linear colonization, severity of infection, and potential regeneration of roots of five tomato genotypes resistant or susceptible to *Phytophthora parasitica*

Genotype	Zoospore encystment[v]	Linear colonization of taproot (cm)[w]	Infection (ppg severity fresh root × 10^3)[x]	Potential root regeneration (Total root length,[y] (cm)
27-1A (R)	17.7 a[z]	2.2 a	2.1 a	910 a
LA1312 (R)	26.0 a	2.4 a	3.2 a	···
CX8303 (R)	25.5 a	6.1 b	6.8 b	832 a
Peto 343 (S)	13.9 a	5.7 b	14.0 c	952 a
6203 (S)	28.8 a	5.9 b	9.7 c	···

[v] Mean number of zoospore cysts per 2 cm of root tip. Mean based on 20 root tips per genotype.

[w] Taproots of seedlings (10 per genotype) were inoculated at the tip with approximately 200 zoospores. After 3 days, roots were sectioned in 1-cm pieces and plated on $P_{10}VP$ agar plates. Data are averages of two experiments.

[x] Root systems were inoculated with 10^6 zoospores and incubated 3 days at which time root systems were macerated, diluted, and plated out on $P_{10}VP$ medium. The number of colonies of *Phytophthora* per plate were counted and propagules per gram fresh weight estimated. Means are based on four replicate pots with four plants per pot.

[y] Total root length of uninoculated plants estimated using grid intersect method 2 wk after root clipping and expressed as a mean root length of five replicates.

[z] Values in a column followed by the same letter do not differ significantly, $P = 0.05$, according to Duncan's multiple range test.

root maceration technique, all three resistant genotypes had significantly fewer propagules per gram of root tissue than did the susceptible cultivars, Peto 343 and 6203 (Table 1). LA1312 and 27-1A had the fewest propagules per gram fresh weight, whereas CX8303 appeared to have an intermediate number of propagules.

Root growth. There were differences between genotypes in root growth after inoculation. In Peto 343, which had the largest root system before inoculation, total length declined during the 4 wk after inoculation, and this genotype had significantly a smaller root system than CX8303 and 27-1A at the termination of the experiment (Fig. 2). In these two genotypes, total root length was constant for 3 wk after inoculation, and there was a significant increase in root length in the fourth week. Root growth was greater in 27-1A than in CX8303. Root length in uninoculated plants of all genotypes increased throughout the experiment and 4 wk after flooding were 2,038, 2,203, and 2,936 cm for CX8303, Peto 343, and 27-1A, respectively. When roots received a mechanical pruning, the potential to regenerate roots 2 wk after clipping was the same in both susceptible and resistant genotypes (Table 1). In all three lines, total root length 2 wk after pruning was 832–952 cm.

DISCUSSION

An understanding of the basis of resistance to *Phytophthora* would be useful in designing breeding strategies. First, it might help in making prudent decisions concerning the source of resistant material used. If well-adapted cultivars possess the same form of resistance as wild material, then it would be sensible to use the former as a source of resistance. Also, if more than one type of resistance is present, then a combination of these resistance mechanisms might lead to a greater level of resistance and possibly a more durable resistant cultivar.

From this study of three resistant genotypes, it appears that at least two different types of resistance to *P. parasitica* exist in tomato. Both mechanisms appear to result in less colonization of roots by the fungus. In both accessions of *L. e.* var. *cerasiforme*, 27-1A and LA1312, *P. parasitica* was detected only a few centimeters from the point of inoculation. Inhibition of lesion extension and hyphal growth have been demonstrated to be important components of resistance to *Phytophthora* in other crops (6,17,23). In the other resistant cultivar, CX8303, and in the susceptible lines Peto 343 and 6203, *P. parasitica* was isolated approximately 6 cm from the inoculated root tip. Yet when entire root systems were inoculated, CX8303 had fewer propagules per gram of root tissue than the susceptible cultivars (Table 1). This suggests that roots of CX8303 may not be as extensively colonized as Peto 343 or 6203 and that perhaps just the outer cortical layers are infected. Histological studies of roots of susceptible and resistant safflower and strawberry inoculated with *Phytophthora* have shown that hyphae penetrate roots of resistant cultivars but are limited to the epidermal and outer cortical layers. In susceptible lines, however, mycelia spread and extensively colonize the vascular tissue (7,12). Similarly, an increase in disease severity in salt-stressed chrysanthemum roots was associated with fungal colonization of vascular tissue, whereas in nonstressed roots *Phytophthora* was limited to the outer three to four cell layers (21). Histological examination of inoculated roots is needed to compare directly the extent of penetration and colonization of roots of resistant and susceptible tomato lines.

Another possible explanation for the differences in the number of propagules per gram of root tissue between cultivars is that *P. parasitica* may form fewer reproductive structures in the *cerasiforme* accessions and CX8303 relative to the susceptible lines. However, in the dilution plating assay, the source of the colonies was not examined, and no distinction was made between mycelial fragments and reproductive or survival structures.

The genotypic differences in root growth after inoculation are possibly a secondary type of resistance resulting from differences in the severity of root infection. In both 27-1A and CX8303, root regeneration was apparent 4 wk after inoculation, whereas in Peto 343 root length declined throughout the experiment (Fig. 2). However, all three lines had an equal capacity to regenerate roots after mechanical clipping (Table 1). Roots of resistant lines that are less heavily colonized may be able to produce healthy lateral roots, whereas roots that are severely rotted may have a limited capacity for root regeneration. Although it may be a secondary type of resistance in 27-1A and CX8303, abundant root growth after inoculation most likely enhances the survival of these lines in infested fields. Root growth has been shown to be important in resistance to *Phytophthora* in citrus and avocado (1,5,11,20) and may be the primary basis of resistance in other tomato lines.

Zoospore encystment on roots was highly variable, and differences were not detected between genotypes. These results are consistent with studies on other crops in which zoospores of *Phytophthora* encysted and penetrated roots of susceptible and resistant cultivars in equal numbers (7–9,15).

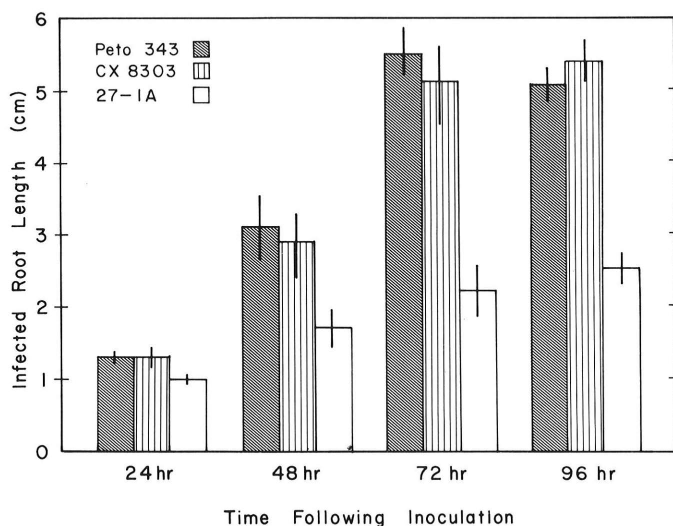

Fig. 1. Linear colonization of taproots by *Phytophthora parasitica* examined at 24-hr intervals for 96 hr after inoculation. Seven to 10 root tips were inoculated with approximately 200 zoospores. At each time interval, roots were sectioned in 1-cm pieces and plated on $P_{10}VP$ agar plates. Data are averages of three experiments, and vertical lines represent standard errors of means.

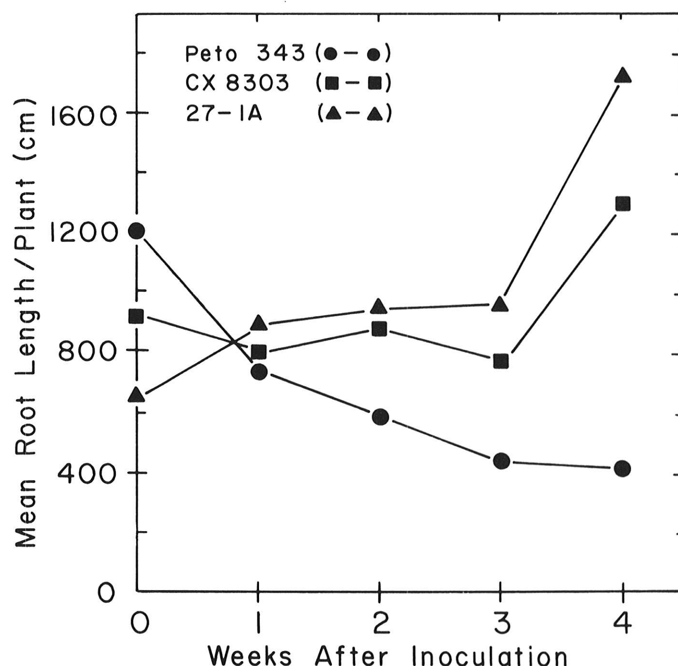

Fig. 2. Root growth of three tomato genotypes after inoculation with 2×10^6 zoospores of *Phytophthora parasitica* per plant. Root growth was measured before inoculation and at weekly intervals after inoculation and was expressed as mean root length per plant, which was estimated using a grid intersect method. Means are based on five replicates.

These results suggest different mechanisms of resistance are present in tomato genotypes from diverse genetic backgrounds. As resistance to *P. parasitica* is detected in other genotypes and the basis of resistance examined, still other types of resistance may be apparent. This may allow for even greater possibilities in developing a high level of durable resistance to Phytophthora root rot.

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