Dispersal of *Phytophthora parasitica* in Tomato Fields by Furrow Irrigation

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ABSTRACT

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Dispersal of *Phytophthora parasitica* from point sources of inoculum buried in irrigation furrows in field plots of processing tomatoes (*Lycopersicon esculentum*) was monitored during five successive irrigations. During the fourth and fifth irrigations, leaf-disk baits floated on the surface of irrigation water became colonized by *P. parasitica* at distances 2, 4, 8, 16, and 32 m downstream from infestation sites, but no leaf disks became colonized 2 m upstream in infested furrows or at any distance in noninfested furrows. Tomato seedlings placed into furrows 50 m downstream from infestation sites became infected during all five irrigations. At the end of the season, incidence of buckeye rot on tomato fruit, caused by *P. parasitica*, increased linearly with logarithmic increases in distance from 0 to 68 m downstream from original points of inoculum. Symptoms of root rot on tomato plants were severe and, with one exception, final populations of *P. parasitica* in the soil under furrows were high only at or very near infestation sites. Shoot symptoms were visible only at an original point of infestation and after the fifth irrigation. Dispersal of the pathogen in irrigation water was most important in development of buckeye rot on fruit. Although the pathogen was also dispersed to roots, the severity of symptoms on roots at distances ≥2 m was generally below that necessary for development of shoot symptoms or yield loss.

Phytophthora root rot of processing tomato (*Lycopersicon esculentum* Mill.) in northern California is caused principally by *Phytophthora parasitica* Dastur (25). The same species also causes buckeye rot of tomato fruit that contact irrigation water or moist soil (13). Dispersal of inoculum within fields may increase the incidence and severity of Phytophthora root and fruit rot in tomato, yet few studies have quantified the dispersal of soilborne *Phytophthora* spp. in annual crops. Shew (27) and Bowers et al (3) described the continuous spread of *P. parasitica* Dastur var. *nicotianae* (Breda de Haan) Tucker and *P. capsici* Leonian originating from point sources within rows of tobacco and pepper, respectively. These studies were done under conditions of high rainfall. Dispersal of *Phytophthora* spp. in an annual crop grown in the absence of rainfall and under furrow irrigation has not been investigated.

Surface water is an important factor for the dispersal of *Phytophthora* spp. (6,7). For example, *P. parasitica, P. citrophthora* (R. E. Sm. & E. H. Sm.) Leonian, *P. cactorum* (Lebert & Cohn) J. Schröt., and other *Phytophthora* spp. have been isolated from irrigation water sources and runoff (5,17,19,20,28,29,30) and have the ability to survive 40–60 days in irrigation waste water (31). Previous reports suggest that *P. cinnamomi* Rands can be transported by water flowing over infested soil in native forests in Western Australia and avocado groves in California (34), from infested to noninfested soil through roads and associated drainage channels constructed within native forests in Victoria (4), in streams carrying runoff water from ohia forests in Hawaii (16,34), and in river networks of the southwestern Cape Province of South Africa (33). Zoospores of *P. cinnamomi* may also be dispersed laterally below the soil surface by water flow—for example, along interfaces between soil horizons in jarrah forests in Western Australia (26).

Increased frequency and duration of furrow irrigations increase the incidence and severity of Phytophthora root and fruit rots in processing tomatoes (13,24). *P. parasitica* sporangia develop in drained soil, and zoospores are released when soil is saturated (1,14). However, although furrow irrigations are likely to stimulate zoospore release and infection, the extent to which *P. parasitica* is physically dispersed by furrow irrigation remains unknown. The objective of this study was to determine the extent to which *P. parasitica* is dispersed along rows of tomato plants from point sources of inoculum by furrow irrigation.

MATERIALS AND METHODS

Plots were established in 1987 and 1989 at the Plant Pathology field area at the University of California, Davis. The experimental sites had no history of Phytophthora root rot, had not been planted to tomatoes for at least 4 yr before the experiments, and did not contain populations of *P. parasitica* detectable by dilution plates or colonization of tomato leaf disks floated above saturated soil (approximate detection thresholds of 3 and 0.4 cfu/g of dry soil, respectively) (21).

The processing tomato cultivar FM6203, which is relatively susceptible to *P. parasitica* (2), was seeded directly on single-row beds with 1.5 m between row centers. Row lengths of 108 m on three adjacent beds and furrows were used as experimental units. Plants were thinned to clumps of two to four plants approximately 20 cm apart. Point sources (actually 0.05 m^2 in area) of inoculum were buried in irrigation furrows on both sides of the center bed 40 m from the upstream end of irrigation furrows, leaving 68 m of row and furrow downstream from original points of inoculum placement. Experimental units with or without point sources of inoculum were replicated four times, arranged in blocks, and separated by two border rows (Fig. 1).

Inoculum. The inoculum was prepared by culturing *P. parasitica* at room temperature (22–26 C) in darkness for 6.5 wk in 0.95-L canning jars containing 500 ml of vermiculite and 250 ml of V8 broth (V8 juice and distilled water, 1:4 [v/v]). Cultures of five individual isolates from five different fields, originally isolated from processing tomato field soils in Yolo County, California (22), were mixed together in equal proportions the day before application to the field. The soil where infestation sites were to be placed was moistened 2 days prior to infestation to create conditions favorable to pathogen survival. Inoculum volume of 2.5 L was placed in each infested furrow 50 days after planting. A trench (45 cm long, 12 cm wide, and 12 cm deep) was dug across each furrow at the point to be infested (Fig. 1), and the inoculum was mixed with the soil used to refill each trench up to a depth of 5 cm to thoroughly bury the inoculum. Extreme care was taken to not contaminate other soil, and noninfested field soil was used to finish refilling the trench to the surface.

Irrigation. Experimental plots were furrow-irrigated the day after infestation (irrigation 1) for 4- to 6-hr duration using methods comparable to conventional furrow irrigation practices. Four successive irrigations (irrigations 2–5) of the same duration were applied on a 14-day schedule until crop maturity.

Detection of *P. parasitica* in irrigation water. Tomato leaf disks cut from processing tomato cultivar FM6203 plants were used as bait to detect the

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pathogen in water. Each trap or sampler consisted of 10 7-mm-diameter tomato leaf disks and an 8 × 5 × 2.3 cm U-shaped styrofoam float enclosed in a 10 × 20 cm nylon mesh bag with 1-mm openings. Bags were attached to plastic pipes long enough to allow placement and removal of the samplers in irrigation furrows without having to step on a bed within an experimental unit. Samplers were transported to and from the field by floating them on water in insulated containers, separated by inoculum treatment, block, and distance.

During each irrigation, samplers were placed at the point of infestation (0 m), 2 m upstream, and 2, 4, 8, 16, and 32 m downstream from the inoculum (Fig. 1) for the entire period in which water was present in the furrow. Samplers were also placed at 2 m upstream and at 0 and 2 m downstream in a noninfested furrow adjacent to the infested furrow (Fig. 1). In the noninfested controls, samplers were placed in the furrows at distances equivalent to the 0- and 32-m locations in infested furrows (Fig. 1). After an irrigation, leaf disks were surface-sterilized for 10 sec with 0.525% NaOCl, rinsed in sterile distilled water, blotted dry, and placed onto Masago selective medium (18). Plates were observed for colony development originating from leaf disks after 5 days of incubation at room temperature in darkness. Colonies of *P. parasitica* originating from infected tomato leaf disks were identified by colony morphology.

Three 3- to 4-wk-old tomato seedlings of cultivar FM6203 were transplanted into both furrows of each experimental unit at a distance of 50 m downstream from the position of inoculum introduction in infested and noninfested furrows before each irrigation (Fig. 1). Before the next irrigation, seedlings transplanted for the previous irrigation were transferred to 18-cm-diameter pots, watered with half-strength Hoagland's nutrient solution (12), and incubated under greenhouse conditions. After 2 wk, roots were rated for severity of disease symptoms, and *P. parasitica* was isolated by the methods below.

Disease evaluation. During the season, all plants in the experiment were assessed on alternate weeks for the incidence of shoot symptoms. At the end of the season, 115 days after planting, three tomato plants were removed at 2 m upstream and 0, 1, 2, 4, 8, 16, and 32 m downstream in the center bed of both infested and noninfested treatments to quantify the severity of symptoms on roots (Fig. 1). Severity of root symptoms was quantified using a scale of 0–4, in which 0 = healthy, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100% of the root system affected. With ratings of 1 and 2, lesions on fine and lateral roots were evident, whereas lesions on lower or upper portions of the taproot were associated with ratings of 3 and 4, respectively. The pathogen was consistently isolated from diseased root tissues on a selective medium (15) amended with 72 μg/ml of hymexazol (Tachigaren 70% wettable powder).

The incidence of buckeye rot on tomato fruit was also quantified at the end of the season by counting the numbers of fruit with buckeye rot per 1-m segment of plant row in the center bed, each segment being centered at the distances used for samplers and at 68 m downstream from points of inoculum. At the time of observation, many fruit on plants in the center bed were in the adjacent furrow because of strong winds earlier in the season (Fig. 1).

Populations of *P. parasitica* in soil. Seven days after the final irrigation, populations of *P. parasitica* were quantified in the soil of the furrows in which samplers had been placed during irrigations (Fig. 1). Four soil cores (1.9 cm in diameter and 15 cm deep) were taken in the centers of furrows at 2 m upstream and at 0, 2, 4, 8, 16, and 32 m downstream from points of inoculum and at equivalent distances of 0, 8, and 32 m downstream in the noninfested furrows. Cores for each distance were mixed to make a composite sample, and all distances and furrows were assayed individually. Dilutions of 40 g of soil plus 160 ml of 0.25% Difco water agar were made, and 1-ml samples were spread onto each of 10 plates of selective medium (15) amended with hymexazol. Plates were incubated in darkness at room temperature (22–26 C) and rinsed with water to remove the soil after 48 hr, and colonies of *P. parasitica* were counted 4, 8, and 12 days after plating. Moisture content of soil samples was measured gravimetrically, and the results are presented as numbers of colony-forming units per gram (cfu/g) of dry soil.

Repeat experiment. The experiment was repeated in 1989 on a different field site using the methods described above, with the following modifications. Volumes of 1.25 L of inoculum were introduced 48 days after planting, and samplers containing leaf-disk baits were placed in control furrows but not in those adjacent to infested furrows. Only 1987 data are illustrated, because relationships between distance from infestation sites and proportions of leaf disks colonized, numbers of fruit with buckeye rot, and severity of root symptoms were similar in 1989.

Statistical analysis. Multivariate repeated measures analysis of variance with Wilks' lambda (λ) statistic was performed with polynomial contrasts to determine the effect of block, inoculum, and distance on proportions of leaf disks

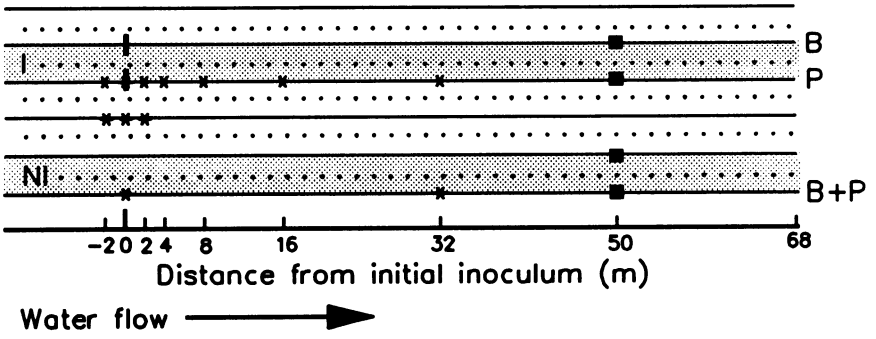

Fig. 1. Diagram of one block within the 1987 experiment showing the position of inoculum introduction (vertical bars), samplers containing leaf-disk baits (x), and transplanted tomato seedlings (■). Irrigation furrows and clumps of plants are represented by horizontal lines and dots, respectively. At the end of the season, the incidence of buckeye rot on tomato fruit was measured in furrow B, and populations of *Phytophthora parasitica* were measured in furrow P. Symptoms on roots of plants in shaded rows were quantified at the same distances that leaf disk and tomato seedling baits were located in infested (I) and noninfested (NI) treatments.

Table 1. Repeated-measures analysis of variance for proportion of leaf disks[a] colonized at various distances from a point source of *Phytophthora parasitica* in irrigation furrows in 1987

	Inoculum and distance effects				Time effects	
Source	df	MS	P	Source	Wilks' λ	P
				Time	0.403	0.0001
Replicate blocks	3	0.081	0.3916			
Inoculum[b]	2	5.970	0.0001	Time*Inoculum	0.282	0.0001
Distance[c]	6	0.392	0.0003	Time*Distance	0.578	0.0297
Error	70	0.080	...			

[a]Transformed as the arcsine of the square root before analysis.
[b]Furrows with, without, or adjacent to furrows with infestation sites.
[c]2 m upstream and 0, 2, 4, 8, 16, and 32 m downstream.

colonized by *P. parasitica*, because the sphericity test was significant (10). Proportions were transformed as the arcsine of the square root to normalize the data before analysis. The effect of distance from the original points of inoculum on the incidence of buckeye rot was determined by linear regression analyses. Means of distance by replicate furrow were transformed as $\ln(x + 2.1)$ to normalize the data before analysis. A three-way analysis of variance was used to determine the effect of block, inoculum, and distance on the severity of root symptoms and populations of *P. parasitica* at the end of the season. Orthogonal polynomial contrasts were performed to determine the effect of distance from the original point of inoculum on severity of root symptoms. Since samples were not taken at all distances for noninfested beds and furrows, interactions with inoculum were not meaningful and therefore not analyzed. Analyses were performed with the General Linear Models and regression procedures in SAS Version 6.03 (SAS Institute, Inc., Cary, NC).

RESULTS

Detection of *P. parasitica* in irrigation water. Averaged across time, percentages of colonized leaf disks were significantly greater in infested than noninfested furrows and varied significantly with distance from original points of inoculum (Table 1). The effects of inoculum and distance on colonized leaf disks also changed through time (Table 1). No tomato leaf disks were colonized during the first irrigation, but disks were colonized at the site of infestation during the second irrigation. Some of the leaf disks downstream from infestation sites were colonized in the third irrigation, and high percentages were colonized at all distances downstream in subsequent irrigations (Fig. 2). Leaf disks were infected in a furrow adjacent to an infested furrow only during the last irrigation. None of the leaf disks placed upstream from original points of infestation in infested furrows or in noninfested control furrows were colonized during any irrigation. Furthermore, tomato seedlings transplanted into furrows at 50 m from infestation sites were infected by *P. parasitica* during all five irrigations, whereas none of the seedlings transplanted into noninfested furrows became infected.

Symptom development. Shoot symptoms of Phytophthora root rot were only visible during the experiment on plants at infestation sites after the final irrigation. In inoculated furrows, the severity of root symptoms was greatest near the site where inoculum was buried, and symptoms decreased with increasing distance from original points of inoculum (quadratically; $P = 0.0009$) (Fig. 3A). No symptoms were observed in rows bordered by control, noninfested

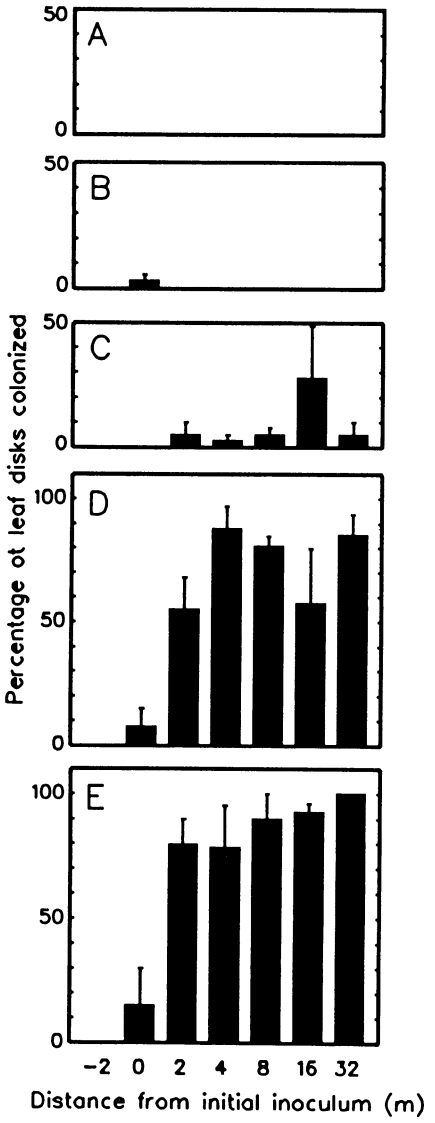

Fig. 2. Percentages of leaf disks colonized during five successive irrigations (**A–E** for irrigations 1–5, respectively) in 1987 plotted as a function of the distance from the site where *Phytophthora parasitica* was buried in irrigation furrows. Negative and positive distances represent locations upstream and downstream from infestation sites (0 m), respectively. Means for four replicate furrows and standard errors are shown.

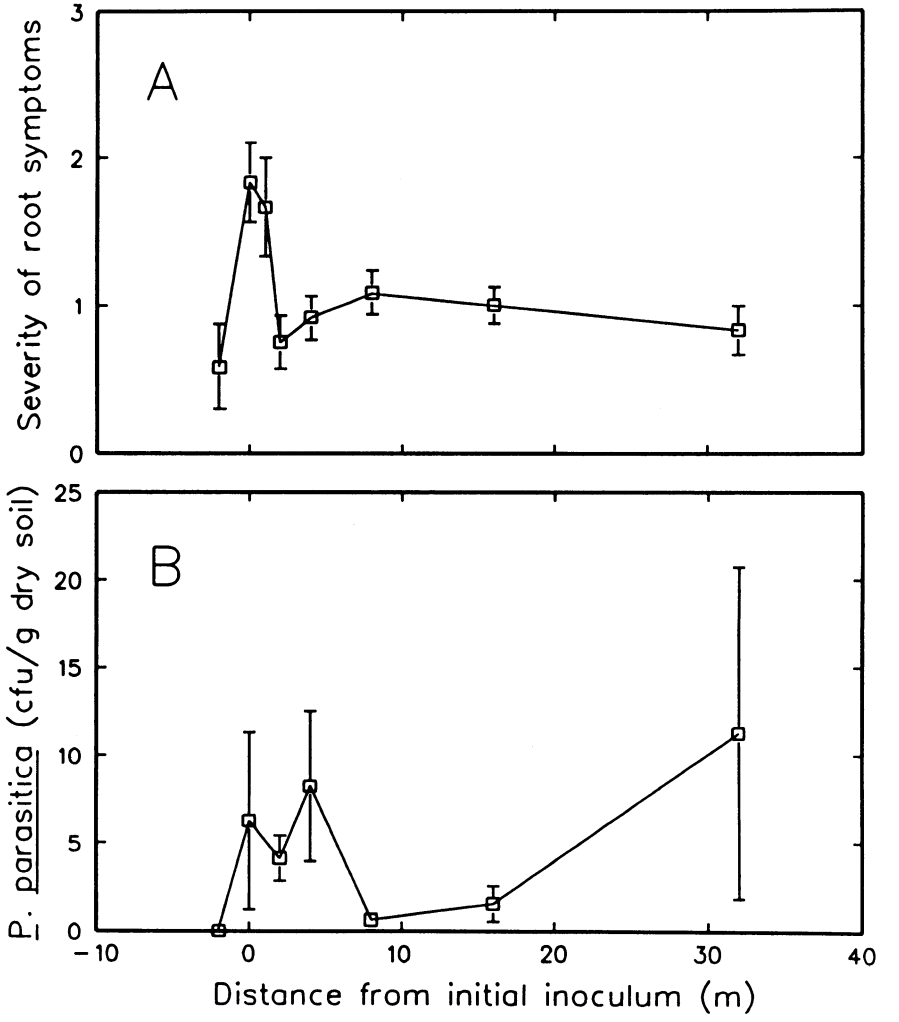

Fig. 3. The final severity of symptoms on roots **(A)** and the final populations of *Phytophthora parasitica* in soil **(B)** at various distances from the sites on which *P. parasitica* was buried in irrigation furrows in 1987. The negative and positive distances represent locations upstream and downstream from infestation sites (0 m), respectively. Severities were measured on a scale of 0–4, and means of four replicate rows or furrows and standard errors are shown.

furrows.

Total numbers of fruit per meter of plant row were similar among control and treatment plots (Neher and Duniway, *unpublished*). In infested furrows, numbers of fruit with buckeye rot increased linearly with logarithmic increases in distance from infestation sites for the entire length of the irrigation furrow (Fig. 4). In noninfested furrows, moderate numbers of fruit (e.g., average of 14/m) were infected at 32 and 68 m downstream, whereas only a few fruit (an average of 2/m) were infected at lesser distances.

Populations of *P. parasitica* in soil. The gradient observed for populations of *P. parasitica* in infested furrows appeared similar to the disease gradient for the severity of root symptoms, with the exception of high populations at 32 m (Fig. 3B). However, populations were not significantly different in regard to inoculum treatment ($P = 0.1611$) or distance from original points of inoculum ($P = 0.1825$). In noninfested furrows, populations of *P. parasitica* (17 cfu/g) were observed at 32 m from infestation sites but at no other distance from points of infestation.

In 1989, similar relationships were found between the distance from infestation sites in infested furrows and the colonization of leaf disks through time, the development of root symptoms on tomato seedlings transplanted into infested furrows at 50 m, and the incidence of buckeye rot on tomato fruit. However, root and shoot symptoms on tomatoes in plant rows were negligible, and populations of *P. parasitica* in soil of furrows were below the threshold for detection on dilution plates at all locations.

DISCUSSION

P. parasitica was disseminated considerable distances in furrows during successive irrigations, as evidenced by detection at the maximum distances from original points of inoculum assayed by each type of bait in the experiment (colonized leaf disks 32 m downstream and infections of tomato seedlings at a distance of 50 m). The dispersal of inoculum was primarily in the direction of water flow; no leaf disks were colonized, no fruit became infected, and only very minor symptoms on roots were observed in locations upstream from infestation sites.

Zoospores are likely to have been the propagule that infected leaf disks floating on the surface of water and tomato fruit laying on the surface. Periods of soil drainage followed by saturation provided conditions favorable for sporangia production and release of zoospores, respectively (1,14,32). Although the results suggest zoospores were dispersed in the irrigation water, the type of propagule infecting roots was not determined in this experiment.

Previous experiments showed that high percentages of green tomato fruit can be infected by *P. parasitica* within one 4- to 6-hr irrigation period (13). In the present study, after five irrigations, numerous fruit were infected by *P. parasitica*, and the numbers infected increased linearly with logarithmic increases in distance from infestation sites. Sources of secondary inoculum likely developed between successive irrigations; an accumulation of secondary inoculum and the unidirectional flow of water in furrows may account for the increase in fruit infection with distance down the irrigation furrows. These factors, coupled with slower drainage at the low end of furrows, might explain the greater incidence and severity of Phytophthora root and fruit rot at the end of furrow rows in commercial fields.

The greatest severity of symptoms on roots was at the original point of inoculum placement, and severities of root symptoms decreased with increasing distance, especially at distances >8 m downstream from infestation sites. Symptoms on shoots were observed only at points of inoculum introduction where root symptoms exceeded a severity rating of 2 (lesions on lateral roots), which is the threshold severity level before shoot symptoms develop (Neher and Duniway, *unpublished*). Shoot symptoms were not observed at distances from infestation sites where the severity of root symptoms was less than 2. At least in this system, levels of root disease within one growing season may be related more to inoculum levels already present in the soil in which plants are growing than to inoculum introduced by dispersal. This may have occurred in part because inoculum must be transported laterally from furrows into the soil comprising the beds before root infection can occur.

Populations of *P. parasitica* detected in soil by dilution plates were relatively low. The high incidence of leaf disk colonization and buckeye rot on fruit in infested furrows, however, suggests that the pathogen was extensively dispersed and would be present at the soil surface. Presumably, water infiltration would disperse propagules into soil within depths sampled in cores. Populations actually detected by dilution plates and selective medium were low, possibly because inoculum infiltration was limited, or because the soil dilution method has a low efficiency of recovery. For example, the approximate threshold for detection of *P. parasitica* on soil dilution plates was 3 cfu/g (21).

Measurements of pathogen populations also suggest that some noninfested furrows were contaminated with *P. parasitica* during the course of the experiment. For example, relatively high populations of *P. parasitica* at 32 m from infestation sites in infested and two noninfested furrows may be attributed to contamination caused by placing and removing transplanted seedlings between treatments before and after irrigations. This conclusion was supported in 1989, when extreme care was taken to prevent contamination between treatments during transplantation, and the pathogen was not detected in noninfested furrows at any time during the season. Contamination likely occurred late in the season, because leaf disks became colonized by *P. parasitica* in noninfested furrows at 32 m from original points of infestation

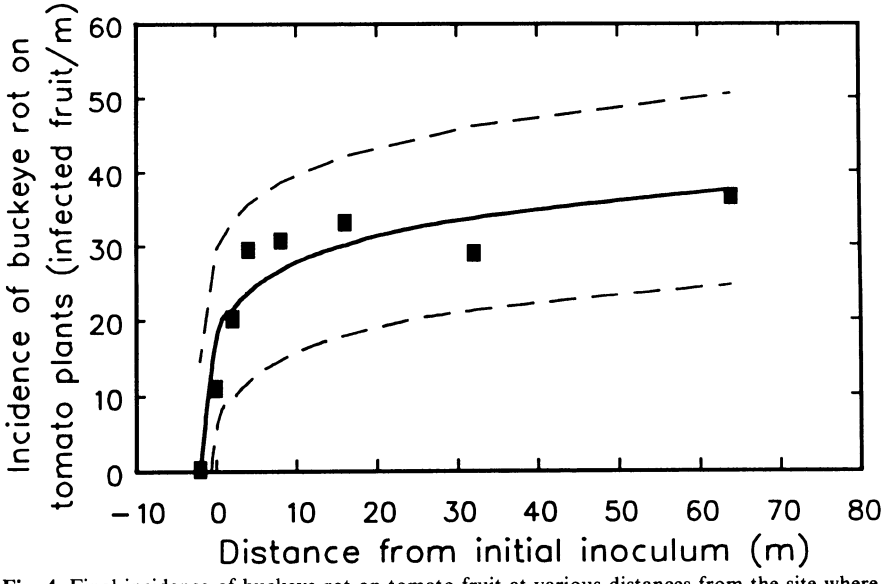

Fig. 4. Final incidence of buckeye rot on tomato fruit at various distances from the site where *Phytophthora parasitica* was buried in irrigation furrows in 1987. Negative and positive distances represent locations upstream and downstream from infestation sites (0 m), respectively. Each value represents the mean of four replicate furrows. The solid line represents a linear regression: buckeye rot = 13.1715 + 5.8528[ln(distance + 2.1)]; $P = 0.0005$, $R^2 = 0.88$. The dashed lines represent the upper and lower 95% confidence limits around the regression line, and nontransformed data are shown.

only during the fifth irrigation. Similarly, infection of approximately 14 fruit per meter at distances of 32 and 68 m in noninfested furrows were probably caused by contamination. However, infection of approximately two fruit per meter at distances <32 m from infestation sites in noninfested furrows is more difficult to explain. There was either a widely distributed but low level of contamination during the experiment or an initial presence of *P. parasitica* in soil at undetectable low levels, or the pathogen was present in the water source used for irrigation. In any case, gradients observed for fruit infection, leaf disk colonization, and root symptoms in infested treatments compared to the near or total absence of gradients in noninfested controls suggest that inoculum dispersal from the introduced inoculum accounts for the results obtained.

The trends observed in 1987 were supported by the replication of the experiment in 1989. However, in 1989 the development of negligible symptoms on tomato roots and lack of detection of populations of *P. parasitica* in soil of furrows could be at least partially attributed to the lower level of initial inoculum at infestation sites and different field location. Furthermore, there was no contamination evident in control furrows. In addition, another study using methods similar to those used in 1989 yielded gradients of disease (i.e., root rot symptoms and incidence of rot on fruit) on tomatoes and peppers from point sources of *P. capsici* (A. Café and J. M. Duniway, *unpublished*) that were similar to those reported here for *P. parasitica* on tomato.

The dispersal gradients observed here for *P. parasitica* differed dramatically from those of air- and splash-dispersed pathogens, including some *Phytophthora* spp., for which inoculum and disease gradients usually decrease steeply from point sources (8,9,11). For example, deposition of splash droplets containing sporangia of *P. cactorum* decreases in number with increasing distance from an original point of inoculum (11,23). In studies of *P. capsici* (3) and *P. parasitica* var. nicotianae (27), relatively high incidences of diseased plants developed, and the pathogens were detected in soil at all distances examined from infestation sites down rows of pepper and tobacco, respectively. In those studies, inoculum was dispersed by rainfall, which could splash inoculum close to the base of the plants, whereas in this study, furrow irrigations would not likely splash inoculum. Maximum distances of disease development from infestation sites were also much shorter (5 m) in the previous (27) than in the present study (68 m).

In conclusion, this study indicates that *P. parasitica* is readily dispersed in irrigation furrows at least 68 m downstream from point sources of inoculum within a field. Dispersal of *P. parasitica* in water is important in the development of buckeye rot on fruit. Although symptoms on roots developed, the severity was generally below that necessary for development of shoot symptoms or yield loss, at least within the duration of the present experiment. Higher levels of inoculum, however, may result in more severe disease development on roots and greater disease spread.

ACKNOWLEDGMENT

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