Relationship Between Amount of *Phytophthora parasitica* Added to Field Soil and the Development of Root Rot in Processing Tomatoes

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ABSTRACT

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Field plots in which *Phytophthora parasitica* was not detected initially were planted to processing tomatoes, and the soil was infested 35 or 45 days after planting in 1987 and 1988, respectively, to give average maximum levels of 1–2, 3–4, 7–28, and 29–65 colony-forming units of *P. parasitica* per gram of soil. Inoculum levels in the four treatments were significantly different when averaged across time between infestation and crop maturity, and disease incidence and severity increased significantly with increasing inoculum levels. For example, final incidences of plants with shoot symptoms were 1.5, 6.4, 14.0, and 24.4% and 0.4, 15.4, 30.2, and 52.3% for the zero, low, intermediate, and high inoculum treatments in 1987 and 1988, respectively. Yield was reduced significantly (20%) only at the highest inoculum level in 1987. However, moderately severe symptoms frequently developed on roots and shoots with low to high levels of inoculum without causing yield losses in both years. Extending furrow irrigations from 4 to 24 h in duration did not significantly affect disease incidence or severity. Crop growth, phenology, and leaf water potentials were not affected significantly by the inoculum or irrigation treatments. The results suggest that development of Phytophthora root rot symptoms on processing tomatoes depended on the inoculum level applied to soil early in the cropping season.

Additional keywords: epidemiology, inoculum level, *Lycopersicon esculentum*.

"Multiple" and "single" cycle diseases have been theoretically differentiated in part by the independence or dependence of epidemic development on initial inoculum levels, respectively (4,28). Soilborne *Phytophthora* spp. may have multiple generations within a cropping season and therefore have the potential to cause "multiple cycle" or "compound interest" diseases (7). Furthermore, if populations of *Phytophthora* increase rapidly by production and dispersal of secondary inoculum, low levels of initial inoculum would have the potential to cause severe disease epidemics in both annual and perennial crops. However, the relationship between level of *Phytophthora* spp. in soil and epidemic development of Phytophthora root rots under field conditions, especially in annual hosts, has not been established conclusively.

In greenhouse experiments with host plants in containers, inoculum levels of *Phytophthora* spp. as low as 0.01 or 0.05 chlamydospores per gram of soil have caused high incidences of host mortality (16,26). In addition, positive relationships between inoculum level and seedling infection or mortality have been observed (18). Few studies, however, have related epidemic development of Phytophthora root rots in the field to inoculum level (9,16,18). In the example of black shank of tobacco, disease incidence was similar in greenhouse and field experiments with an initial inoculum level of 0.5 chlamydospores of *P. parasitica* var. *nicotianae* per gram of soil (16).

Production and dispersal of secondary inoculum by *Phytophthora* spp. in soil are highly dependent on soil matric potential and temperature (5,6,15,17). In laboratory experiments, brief periods of saturation (0.5–24 h at 0 to −1 kPa matric potential), preceded and followed by lower matric potentials (−3 or −5 kPa), altered the relationship between inoculum level and development of black shank in tobacco (25), probably because saturation favors indirect sporangial germination and zoospore dispersal (2,5,6). In the field, irrigations saturate at least some of the soil, and

increased frequency and duration of furrow irrigations have been found to increase the incidence and severity of Phytophthora root and fruit rots in processing tomatoes (6,14,22).

In this study, field experiments were conducted to test the hypothesis that a pathogenic and soilborne *Phytophthora* spp., when added to soil in different amounts, would cause contrasting levels of root rot to develop in an annual crop. Processing tomatoes (*Lycopersicon esculentum* Mill.) grown under furrow irrigation, and *Phytophthora parasitica* Dastur, a root and fruit pathogen of tomato (24), were used as the model system. Effects of extended periods of furrow irrigation on epidemic development also were examined, and disease impacts on plant water potential, phenology, growth, and harvestable yield were measured. A preliminary report of this work was published (20).

MATERIALS AND METHODS

Inoculum. Soil samples were collected from tomato fields in Yolo County, California, during March 1987, and *P. parasitica* was isolated using green tomato fruit as bait (15). Isolates were identified as *P. parasitica* according to Waterhouse (29), and all were found to be highly pathogenic to tomato seedlings (D. Neher and J. M. Duniway, *unpublished data*). Cultures were maintained on cornmeal agar slants or V8 agar plates (200 ml of V8 juice, 17 g of Difco agar, 2 g of $CaCO_3$, and 800 ml of sterile distilled water per liter) at 25 C.

Inoculum for field experiments was prepared by culturing *P. parasitica* at room temperature (22–26 C) in darkness for 5.5–6.5 wk in 0.95-L canning jars containing 500 ml of vermiculite and 250 ml of V8 broth. The colonized vermiculite medium contained a mixture of sporangia, chlamydospores, and mycelium. Cultures of five isolates, each from a different commercial tomato field, were mixed together in equal proportions the day before application to the field. Inoculum was used undiluted or serially diluted by volume with moist vermiculite. Mixtures and dilutions were prepared using a 28.4-L food mixer (Kitchen Aid, Inc., St. Joseph, MI).

Field experiments. Experiments were conducted in field locations with Rieff clay loam and sandy loam soils in 1987 and 1988, respectively, at the University of California, Davis. Processing tomato cultivar FM6203 was seeded directly on single-row beds with 1.5 m between row centers and was furrow irrigated as needed. Two adjacent beds, each with a row segment length of 13.1 m and 5–9 border plants at each end, were used as experimental units. Plants were thinned to one per 20 cm of row 28–35 days after planting, which gave approximately 62 plants for data collection in each row.

The sites had not been planted to tomatoes for at least 4 yr before the experiments and did not contain populations of *P. parasitica* detectable by either dilution plates or colonization of tomato leaf disks floating above saturated soil (approximate detection thresholds of 3 and 0.4 cfu/g of dry soil, respectively; 19). Plots were infested with the fungus 35 or 42 days after planting in 1987 and 1988, respectively, by incorporating colonized vermiculite in the soil with a cultivator approximately 15 cm from the plants on both sides of each row. Plants were infested after emergence (15 cm tall) to prevent damping-off and to establish a uniform plant stand. The beds were originally established so that the infestation procedures would cause a minimal disturbance of roots. The four inoculum treatments received cultured vermiculite inoculum in volumes of 343 (high), 34.3 (intermediate), 3.43 (low), and 0 (zero) cm^3/m on each side of the row. Relative differences between inoculum treatments were confirmed by plating final dilutions of vermiculite inoculum on selective medium (16) and counting zoospores released from vermiculite after subsequent periods of chilling and warming, respectively (21).

The beds were reshaped immediately after infestation and irrigated uniformly for 4 h within 48 h after infestation (22). Subsequent irrigations were initiated 2 wk later and were applied 49, 63, 77, and 91 days after planting in 1987 and 57, 70, 85, and 98 days after planting in 1988. In one irrigation treatment, water was applied to the furrows for 4–6 h in every irrigation (standard irrigation). In the second irrigation treatment, the second and fourth irrigations were the same as the standard irrigations, but the first and third irrigations were extended to maintain water in the furrows for 24 h to more fully saturate the beds (extended irrigations). The treatments were arranged in a split plot design, with irrigation treatments as the main plots and the four inoculum levels as subplots. Each treatment was replicated within each of four blocks, and each experimental unit was irrigated separately after soil was infested.

Quantification of inoculum in soil. Soil in each plot was sampled biweekly, always 5 days after irrigation except for the first sample, which was taken immediately after infestation. Five soil cores (1.9 cm in diameter and 25 cm deep) were taken in a stratified random pattern approximately 15–20 cm from alternate sides of the plant row. The top 5 cm of each core was discarded, and the remaining soil was bulked into a single composite sample per plot. Composite soil samples were mixed, stored at the existing moisture and temperature, and processed for dilution plating within 10 h after sampling to minimize changes in pathogen populations.

Subsamples from plots with high and intermediate inoculum levels were diluted with 0.25% Difco water agar to give 1:5 (40 g of soil/160 ml of water agar) and 1:10 dilutions (100 ml of 1:5 mixture/100 ml of water agar). Subsamples from plots uninfested or with the low inoculum treatment were diluted only 1:5 in water agar. From each dilution, 1 ml was spread onto each of 10 plates of selective medium (16) amended with 72 μ of hymexazol per milliliter (Tachigaren, 70% wettable powder, Sankyo Co., Yasu, Shiga-Ken, Japan). Plates were incubated in darkness at room temperature (22–26 C). Plates were rinsed with water to remove the soil after 48 h, and colonies of *P. parasitica* were counted 4, 8, and 12 days after plating. Moisture content of soil samples was measured gravimetrically, and data were transformed to number of colony-forming units per gram (cfu/g) of dry soil.

Epidemic development and plant growth. Within each experimental unit, plants in one row were left undisturbed to be repeatedly observed for incidence and severity of disease symptoms on shoots (leaves plus stems) and for a final harvest of fruit. The second row within each experimental unit was divided into eight 1.64-m long quadrats for destructive sampling. Quadrats were assigned so that equal numbers of quadrats at every distance from the irrigation source were sampled within each treatment and experimental block at each sampling time. The central three plants within a single quadrat per experimental unit were assessed for incidence and severity of symptoms on shoots and roots, six or seven times during the season. Twelve plants per treatment were evaluated at each sample time in destructively sampled rows. Severity of shoot and 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 shoot or root system affected. On shoots, wilting was generally apparent in plants with ratings of 1 and 2, and chlorosis and/or necrosis were visible for plants with ratings of 3 and 4. On roots with ratings of 1 and 2, lesions on fine and lateral roots were evident, whereas lesions on lower or upper portions of the tap root were associated with ratings of 3 and 4, respectively. Shoot symptoms were always evaluated first, then the sampled plants were cut at ground level, and the roots from 0–30 cm depth were removed for assessment of symptoms. Although data were recorded for individual plants, ratings of symptoms on shoots and roots of the same plant were made independently.

Phenology and biomass were measured on the plants removed from destructively sampled rows of plots receiving zero, intermediate, and high levels of inoculum using the methods described by Ristaino et al (23).

At maturity, the previously undisturbed row in each experimental unit was harvested, and fresh weight of red fruit that were either unblemished, had less than 50% sunburn, or had minor blossom end rot were totaled for each plot to obtain a measure of harvestable yield comparable to those obtained in commercial

production. In 1988, size, pH, and soluble solids of red fruit were determined by the Processing Tomato Quality Lab at University of California, Davis.

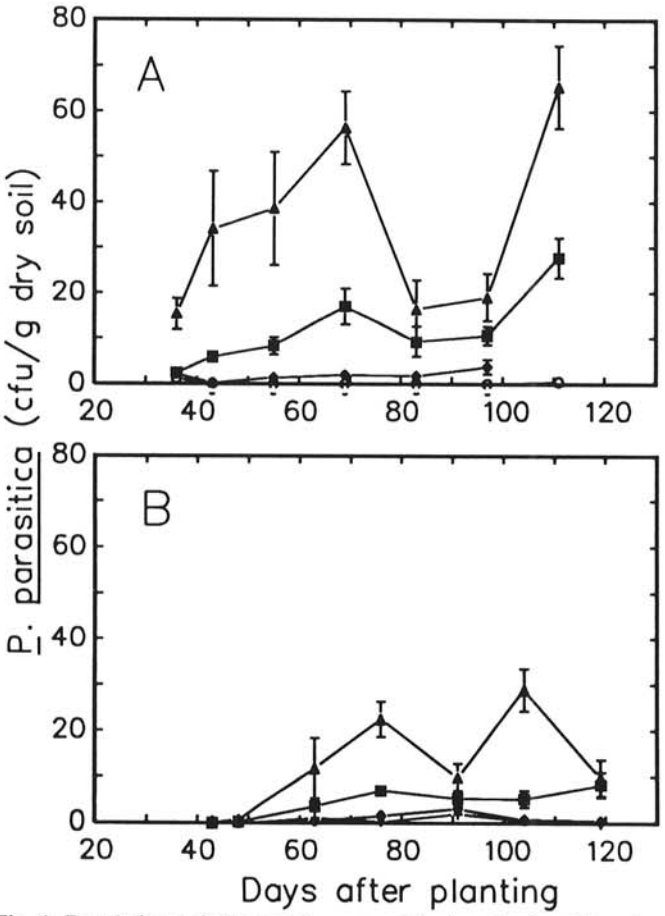

Fig. 1. Populations of *Phytophthora parasitica* in soil after infestation of field plots 35 and 42 days after planting tomatoes in 1987 and 1988, respectively. Inoculum treatments were high (▲), intermediate (■), low (◆), and zero (○) in 1987 (**A**) and 1988 (**B**). Each value represents the mean of eight replicate plots, averaged across the two irrigation treatments. Standard error bars that are not visible are smaller than the symbols. Note that the low inoculum treatment was not sampled for the last period in 1987.

Water relations. Predawn and midday leaf water potentials were measured before each irrigation with a pressure chamber (22). The duration of saturated soil conditions in the beds immediately after the last two irrigations was monitored with tensiometers fitted with mercury manometers in 1987 and with pressure transducers in 1988 (3). Tensiometer cups were placed in soil at a depth of 20 cm in the undisturbed plant row, midway between the row and furrow, and in the furrow of one plot for each of six treatments. The treatments measured were those receiving zero, intermediate, and high levels of inoculum, and furrow irrigated with either standard or extended durations. Soil bulk densities and moisture characteristic curves (13) for both the 1987 and 1988 field sites were determined by removing undisturbed soil cores (76 mm long, 76 mm diameter) at four positions in each site with the top of the core equivalent to a 20-cm depth (19).

Statistical analysis. Symptom data from destructively and nondestructively sampled rows were analyzed separately, and all analyses were treated as a balanced split-plot design and performed with SAS 6.04 (SAS Institute, Inc., Cary, NC). Shoot symptoms in nondestructively and destructively sampled rows, root symptoms in destructively sampled rows, and pathogen populations in nondestructively sampled rows were analyzed as repeated-measures analysis of variance using General Linear Models (GLM) procedures. Pathogen populations (cfu/g) were transformed as $\log_{10}(x + 1)$ to normalize data before analysis. Sphericity tests were significant except for three of 14 cases; therefore the multivariate repeated measures analysis of variance with Wilks' lambda (λ) statistic was used. All treatment effects through time were tested with the residual sums of squares and cross products matrix, because there were insufficient degrees of freedom to calculate the error term ($error_a$) for the interaction of time with irrigation (11). Final fruit yield in the undisturbed rows was analyzed using GLM procedures, and means were separated by orthogonal contrasts.

RESULTS

Propagule levels averaged 1.2, 2.1, 2.4, and 15 in 1987 and 0, 0, 0, and 0.3 cfu/g of dry soil in 1988 immediately after infestation for the zero, low, intermediate, and high inoculum treatments, respectively (Fig. 1). However, when averaged across all sampling times, populations were significantly different, ranking in the same order as volumes of cultured vermiculite inoculum added to the soil (Table 1). The effect of inoculum treatment on populations varied significantly through time in 1988, but not in 1987 (Table 1). Populations increased to maxi-

TABLE 1. Effect of irrigation and level of inoculum, added 35 or 42 days after planting in 1987 and 1988, respectively, on subsequent populations[a] of *Phytophthora parasitica* in processing tomatoes[b]

	Irrigation and inoculum effects				Time effects	
Source	df	MS[c]	*P*	Source	Wilks' λ	*P*
1987						
				Time	0.524	0.0775
Replicate blocks	3	0.341	0.0190			
Irrigation[d]	1	0.122	0.0812	Time*irrigation	0.783	0.5836
$Error_a$	3	0.018				
Inoculation[e]	3	12.231	0.0001	Time*inoculation	0.223	0.0576
Irrigation*inoculation[f]	3	0.089	0.3639	Time*irrigation*inoculation	0.580	0.8819
$Error_b$	18	0.079				
1988						
				Time	0.046	0.0001
Replicate blocks	3	0.282	0.0569			
Irrigation	1	0.002	0.8043	Time*irrigation	0.520	0.1719
$Error_a$	3	0.034				
Inoculation	3	4.579	0.0001	Time*inoculation	0.047	0.0004
Irrigation*inoculation	3	0.074	0.6623	Time*irrigation*inoculation	0.166	0.0889
$Error_b$	17	0.138				

[a] Log_{10} (cfu + 1).
[b] Repeated-measures analysis of variance table.
[c] Mean squares.
[d] Standard and extended furrow irrigations.
[e] Zero, low, intermediate and high inoculum levels.
[f] Interaction between irrigation and inoculum treatments.

mum levels of 1.2, 3.8, 27.9, and 65.4 cfu/g in 1987 and 1.9, 2.9, 7.1, and 28.8 cfu/g of dry soil in 1988 in the zero, low, intermediate, and high inoculum treatments, respectively. Irrigation treatments did not significantly effect populations (Table 1).

In undisturbed rows, the four inoculum levels applied resulted in four significantly different levels of incidence (Table 2) and severity (F test, $P = 0.0085$ and Wilks' λ, $P = 0.0215$ in 1987; F test, $P = 0.0001$ and Wilks' λ, $P = 0.0001$ in 1988) of shoot symptoms. Sometimes, earlier epidemic initiation, more rapid development, and always greater final levels of disease incidence and severity were observed in the high inoculum treatment compared to zero, low, and intermediate inoculum levels (Fig. 2). Final incidences of shoot symptoms were 1.5, 6.4, 14.0, and 24.4% and 0.4, 15.4, 30.2, and 52.3% for the zero, low, intermediate, and high inoculum treatments in 1987 and 1988, respectively.

TABLE 2. Effect of irrigation and level of inoculum, added 35 or 42 days after planting in 1987 and 1988, respectively, on the incidence (%) of symptoms on shoots of processing tomatoes in nondestructively sampled rows[a]

	Irrigation and inoculum effects				Time effects	
Source	df	MS[b]	P	Source	Wilks' λ	P
1987						
				Time	0.098	0.0001
Replicate blocks	3	145.1	0.7438			
Irrigation[c]	1	140.5	0.5623	Time*irrigation	0.634	0.3436
$Error_a$	3	333.2				
Inoculation[d]	3	1421.9	0.0031	Time*inoculation	0.134	0.0246
Irrigation*inoculation[e]	3	120.5	0.6420	Time*irrigation*inoculation	0.203	0.1222
$Error_b$	18	211.4				
1988						
				Time	0.073	0.0001
Replicate blocks	3	36.8	0.9700			
Irrigation	1	171.0	0.5990	Time*irrigation	0.342	0.0148
$Error_a$	3	497.9				
Inoculation	3	8532.7	0.0001	Time*inoculation	0.036	0.0001
Irrigation*inoculation	3	378.6	0.2168	Time*irrigation*inoculation	0.286	0.3465
$Error_b$	18	231.8				

[a] Repeated-measures analysis of variance table.
[b] Mean squares.
[c] Standard and extended furrow irrigations.
[d] Zero, low, intermediate, and high inoculum levels.
[e] Interaction between irrigation and inoculum treatments.

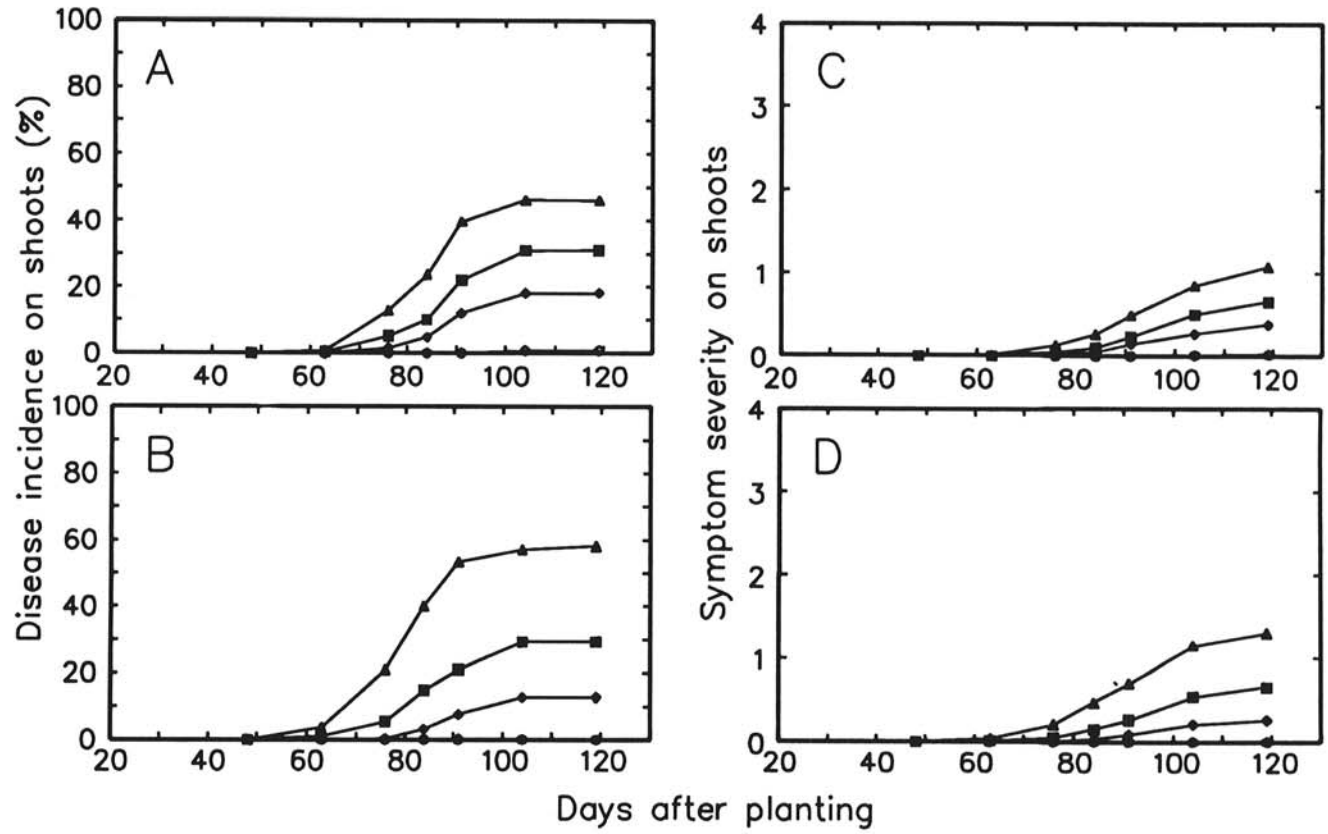

Fig. 2. Progression of Phytophthora root rot on processing tomatoes in nondestructively sampled rows infested with various levels of *Phytophthora parasitica* in 1988: **A, B,** disease incidence, and **C, D,** severity of symptoms on shoots (scale of 0–4) plotted as a function of days after planting. Inoculum treatments were high (▲), intermediate (■), low (◆), and zero (○) amounts of *P. parasitica*, added 42 days after planting, with furrow irrigation treatments of either standard (**A,C**) or extended (**B,D**) duration.

Only 1988 symptom data are illustrated (Fig. 2), because disease levels were in the same ranking as added inoculum levels at most times of observation in both years. In 1987, symptom severity increased later in the season, and in the highest inoculum treatment, the final severities were greater compared to 1988. In contrast, the incidence of plants with mild symptoms was greater in 1988 than in 1987. Extending furrow irrigations from 4 to 24 h in duration did not significantly affect disease incidence or severity although there was a trend in 1987 indicating that extended irrigations increased incidence and severity of shoot symptoms in the intermediate inoculum treatment.

Epidemic development in the destructively sampled rows also varied with the inoculum level applied. As in the undisturbed rows, both the incidence and severity of symptoms on shoots increased significantly with increasing inoculum level in both years (incidence: F test, $P = 0.0143$ and Wilks' λ, $P = 0.0040$ in 1987; F test, $P = 0.0001$ and Wilks' λ, $P = 0.0021$ in 1988. severity: F test, $P = 0.0007$ and Wilks' λ, $P = 0.0001$ in 1987; F test, $P = 0.0001$ and Wilks' λ, $P = 0.0001$ in 1988). Root symptoms in destructively sampled rows were sometimes apparent as early as 9 days after the soil was infested, and the incidence and severity of root symptoms generally increased with increasing inoculum level applied (Fig. 3) (incidence: F test, $P = 0.0001$ and Wilks' λ, $P = 0.0209$ in 1987; F test, $P = 0.0001$ and Wilks' λ, $P = 0.0001$ in 1988. severity: F test, $P = 0.0001$ and Wilks' λ, $P = 0.0001$ in 1987; F test, $P = 0.0001$ and Wilks' λ, $P = 0.0001$ in 1988). Symptoms developed earlier and were relatively more severe on roots than on shoots, and extended irrigations did not significantly increase development of root symptoms. The pathogen was consistently isolated from diseased root tissues on a selective medium (16).

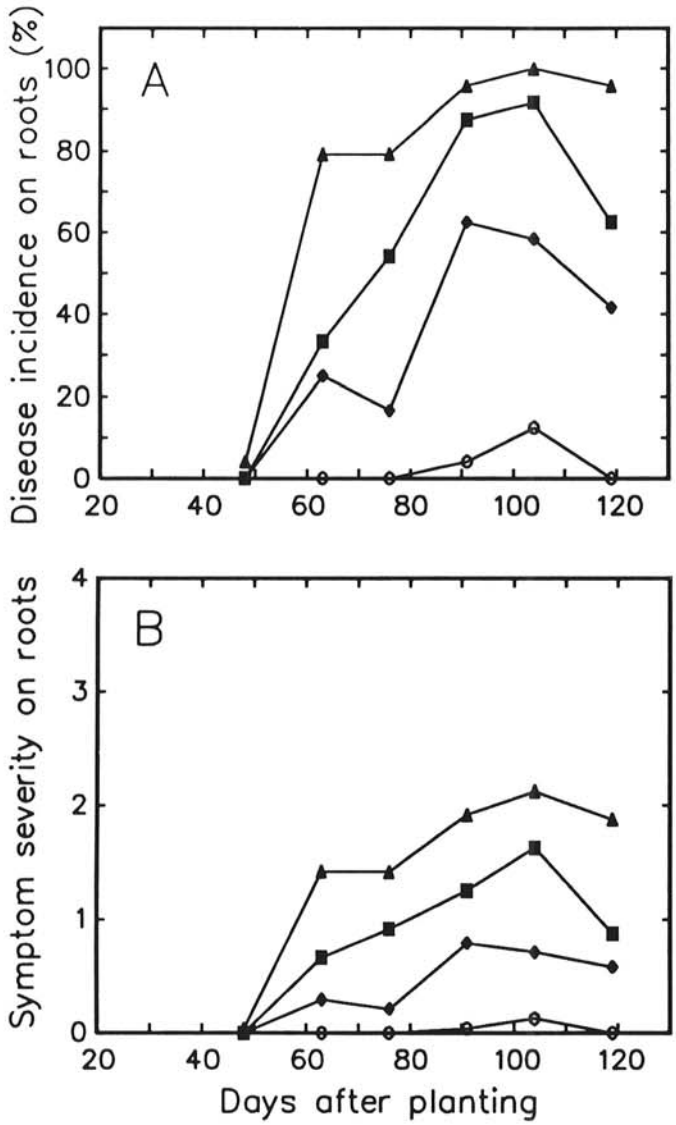

Fig. 3. Progression of Phytophthora root rot on processing tomatoes in destructively sampled rows infested with various levels of *Phytophthora parasitica* in 1988: **A,** disease incidence and **B,** severity of symptoms on roots (scale of 0–4) plotted as a function of days after planting. Inoculum treatments were high (▲), intermediate (■), low (◆), and zero (○) amounts of *P. parasitica*, added 42 days after planting. Each value represents the mean of eight replicate plots, averaged across the two irrigation treatments.

Crop growth and phenology in both years did not differ significantly between inoculum or irrigation treatments (19; data not shown). Further, none of the treatments altered leaf water potentials measured midday and predawn before irrigations in 1987 and 1988 (19; data not shown). Tensiometers confirmed that extended irrigations saturated more soil for longer than did normal irrigations (19). Although there were minor differences between years, the overall trends of crop development and water status were similar to those reported previously for healthy processing tomatoes grown under similar conditions (22,23).

In 1987, the highest inoculum level reduced harvestable yield by 20% ($P = 0.0140$), whereas in 1988, there was no significant inoculum effect on yield ($P = 0.0750$). Average harvestable yields for the zero, low, intermediate, and high inoculum treatments were 196.7, 203.7, 195.3 and 154.2 kg per plot in 1987 and 121.1, 120.1, 117.6, and 105.3 kg per plot in 1988, respectively. The average harvestable yield in noninfested rows was equivalent to 93.9 and 58.1 metric tons per hectare for 1987 and 1988, respectively. In neither year was there an irrigation effect on yield ($P = 0.4974$ in 1987 and $P = 0.8360$ in 1988) (19; data not shown). In 1988, fruit soluble solids, pH, and size were 5.13 Brix, 4.34, and 25 fruit per 2 kg, respectively; they were unaffected by the treatments (data not shown).

DISCUSSION

In multiple cycle diseases, it is usually thought that small amounts of inoculum are sufficient to cause severe epidemic development. However, for Phytophthora root rot on processing tomatoes, a potentially multiple cycle disease, the conditions for pathogen growth, reproduction, and dispersal are probably rarely even close to the optimum, especially in soil (6). If conditions were optimum in the tomato cropping system under furrow irrigation, rapid increases in pathogen populations would be expected. Furthermore, relatively low levels of inoculum early in the season would be expected to cause severe epidemics. Instead, four levels of inoculum, added 35 or 42 days after planting, resulted in four different levels of disease incidence and severity. In addition, the four levels of inoculum were significantly different through time, and population increases between 50 and 120 days after planting did not have the kinetics expected with multiple secondary infections. Like others (8,22), we are unable to explain the short-term fluctuations in populations of *P. parasitica* in soil.

Maximum population levels measured after infestation of field soils in this study were similar to those reported for *P. parasitica* in citrus groves (8), but lower than for *P. p. nicotianae* in tobacco fields (16). Populations of *P. parasitica* in citrus groves were relatively low in winter and spring months and increased to maximum levels in July or August (8). The increases may be related to the presence and activity of the host (1), because in contrast to the other treatments (Fig. 1), populations of *P. parasitica* added to soil without the tomato host decreased to levels below those detectable by dilution plates within 3 wk (D. Neher and J. M. Duniway, *unpublished data*). This phenomenon also was reported for *P. p. nicotianae* normally pathogenic on tobacco (10).

The inoculum level treatments in this study were comparable to those reported in other field studies of soilborne *Phytophthora* spp., with the exception of the high inoculum level treatment, which was greater (9,16). However, mortality of processing tomatoes was less at the high inoculum treatment than for other hosts at lower inoculum levels of *Phytophthora* spp. For example, mortality of susceptible tobacco plants was 33–100% when

transplanted into soil with 0.2–0.75 cfu/g of *P. p. nicotianae* (9,16), and there was 50% mortality of Fraser fir trees in soils with 1–30 cfu/g of *P. cinnamomi* (12). Disease relationships to low pathogen populations in soil are less clear, perhaps because estimations of *Phytophthora* populations in field soils may be imprecise when measured by dilution plates. Soil dilutions on selective media may suffice for species that occur in high populations (27), but *Phytophthora* populations are often lower than the threshold of detection (19).

High soil moisture and poor drainage are known to favor *Phytophthora* root rots (e.g., 6), and increased frequency and duration of furrow irrigations accelerated epidemic development caused by *P. parasitica* on the same cultivar of processing tomatoes in a previous study (22). In the present study, irrigation treatments did not affect epidemic development, even though the high inoculum level and the standard and extended furrow irrigation treatments were comparable to the infested and "normal" and "prolonged" irrigation treatments in the former study (22). Perhaps the effect of irrigation treatment was influenced by the level of epidemic development, which differed between the two studies. Root and shoot symptoms developed more rapidly and resulted in greater final disease severities in previous studies in which irrigation had a larger effect (22,23) than in the present study. The difference between the two studies suggests that conditions other than those associated with irrigation limited epidemic development in the present study, including perhaps temperature (19) and inoculum level.

In both the previous (22,23) and present studies, disease effects on processing tomatoes were not measurable until symptoms were visible and physiological effects subsequently increased with disease severity. Adjustments in plant water status, phenology, biomass allocation patterns, and yield were observed in epidemics more severe than in the present study (22,23), and the results reported here indicate that processing tomatoes can sustain mild to moderate symptoms on roots and shoots without exhibiting a yield loss. Yield losses were observed exclusively in the high inoculum treatment in 1987, suggesting that an inoculum threshold for yield loss may exist. However, in 1988, the yield in the noninfested treatment was lower than in 1987, indicating that factors other than disease limited yield.

In conclusion, the present study suggests that epidemic development of Phytophthora root rot in processing tomato is dependent on inoculum level present in soil early in the cropping season. Different levels of inoculum added to the soil early in the season were significantly different averaged across time and gave significantly different levels of disease incidence and severity. Furthermore, tomato plants developed mild to moderate disease levels of Phytophthora root rot before adjustments of leaf water potential, crop phenology, biomass allocation, or yield occurred. Although the results suggest that epidemic development of Phytophthora root rot and yield loss in processing tomatoes are dependent on amount of *P. parasitica* applied to soil early in the cropping season, more direct experimentation is needed to determine the precise nature of disease relationships to inoculum level, present at or before the time of planting.

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