

## Influence of Frequency and Duration of Furrow Irrigation on the Development of Phytophthora Root Rot and Yield in Processing Tomatoes

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This research was supported in part by the University of California Statewide Integrated Pest Management Project.

Accepted for publication 1 August 1988 (submitted for electronic processing).

### ABSTRACT

Ristaino, J. B., Duniway, J. M., and Marois, J. J. 1988. Influence of frequency and duration of furrow irrigation on the development of *Phytophthora* root rot and yield in processing tomatoes. *Phytopathology* 78:1701-1706.

Processing tomatoes grown in field plots with soil either infested or uninfested with *Phytophthora parasitica* were furrow irrigated for 4–8 hr every 14 days (normal irrigation), for 4–8 hr every 28 days (less frequent irrigation), or with alternating 4–8-hr and 24-hr irrigations every 14 days (prolonged irrigation). Disease developed more rapidly and symptom severity was significantly greater on shoots and roots of plants in infested soil that received prolonged irrigations compared with plants that were irrigated less frequently. Midday leaf water potential was reduced significantly as symptom severity increased and, by 90 days after planting,

was correlated negatively with fruit yield at harvest (122 days). Disease significantly reduced fruit yield by 68 or 74%, 34 or 60%, and 20 or 43% as compared with uninoculated controls in prolonged, normal, or less frequent irrigation treatments in 1985 or 1986, respectively. Populations of *P. parasitica* in soil increased from 6 to 17 colony-forming units per gram (cfu/g) of soil after infestation to 67–121 cfu/g of soil at harvest. Results clearly show that variations in the frequency and duration of furrow irrigation can have large effects on the development of *Phytophthora* root rot and yield loss to root rot in processing tomatoes.

*Additional keywords:* crop loss assessment, epidemiology, *Lycopersicon esculentum*, plant water relations.

Phytophthora root rot of processing tomatoes (*Lycopersicon esculentum* Mill.), primarily caused by *Phytophthora parasitica* Dastur., is a serious and widespread disease in California. The duration of saturated conditions in California tomato fields depends on irrigation practices, since little rainfall occurs during the growing season. Although many growers are optimizing yield through irrigation in uninfested fields, in soil infested with *Phytophthora*, improved irrigation scheduling is needed to reduce disease. Better management of the disease in California requires more specific knowledge of irrigation effects on disease development and yield loss, because genetic resistance and chemical controls are not completely effective (5,15). Although saturated soil conditions are known to increase the severity of many *Phytophthora* root rots (10), only a few studies have attempted to quantify effects of irrigation or soil water status on disease progress under field conditions (11,29,30).

Several species of *Phytophthora* have been shown to require saturated conditions for zoospore release and dispersal in soil (10). Saturated soil conditions not only have a direct effect on pathogen behavior but can predispose some plants to more severe disease, as has been shown with *Phytophthora* root rot of alfalfa and rhododendron (4,19). On the other hand, water stress also can predispose several hosts, including tomato seedlings, to more severe *Phytophthora* root rot (1,4,9,30). Although a number of studies have examined the effects of water status on the behavior of *Phytophthora* spp. in soil or the development of *Phytophthora* root rot (10), only a few studies included isolates of *P. parasitica* pathogenic to tomato. Buckeye rot of green tomato fruit caused by *P. parasitica* was found to increase with increased frequency of furrow irrigation in the field (13). At constant soil matric potentials ( $\psi_m$ ), *P. parasitica* forms significant numbers of sporangia at  $\psi_m$  values as low as –300 millibars (mb). However, if mycelial disks are held in soil for a few days at  $\psi_m$  values of –200 to –300 mb, they form large numbers of new sporangia within hours of wetting the soil to saturation (3).

In the present study, field experiments were conducted to evaluate the influence of variations in the frequency and duration of furrow irrigation on the development of *Phytophthora* root rot

and yield in processing tomatoes. A preliminary report of this work has been published (2).

### MATERIALS AND METHODS

**Inoculum preparation.** Soil was collected from 11 tomato fields in Yolo County, CA, during December 1984. *P. parasitica* was isolated readily from 10 of the 11 fields with green tomato fruit as bait (16). Isolates were identified as *P. parasitica* according to Waterhouse (28). Cultures of the fungus were maintained on cornmeal agar slants or V-8 agar plates (800 ml of water, 200 ml of V-8 juice, 2 g of CaCO<sub>3</sub>, and 15 g of agar). All isolates tested were pathogenic on tomato seedlings in greenhouse experiments.

Inoculum for field experiments was prepared by culturing the fungus at room temperature for 4 wk in 1-L canning jars containing 500 ml of vermiculite and 250 ml of V-8 broth. Cultures of five individual isolates from different fields were mixed together in equal proportions immediately before application to the field as inoculum.

**Irrigation experiments.** Experiments were done in 1985 and 1986 at two field locations on clay loam soil at the University of California, Davis. Seed of processing tomato cultivar Ferry Morse 6203 was direct-seeded on single-row beds and irrigated by split furrows (22). Plants were thinned to one per 22.5 cm of row 28 days after planting. Experimental plots were 12.2 m long in 1985 and 13.7 m long in 1986.

Because detectable populations of *P. parasitica* were not present in the soil, some plots were infested artificially with the fungus 42 days after planting at the time larger beds were formed. Infestation at this time allowed treatments to be imposed on a uniform stand of plants. The entire field was irrigated 1 wk before soil infestation with the pathogen, and then allowed to drain to about field capacity. Cultures on V-8 vermiculite medium were incorporated with a cultivator at a rate of 500 cm<sup>3</sup> per 1.2 m of row approximately 20 cm from the plant on both sides of each infested plot. Beds were reshaped (1.5-m centers) immediately after infestation, and all plots were irrigated uniformly again for 4 hr 1 or 2 days after soil infestation (22). Subsequent irrigations, begun 2 wk later, were applied differentially among the treatments arranged in a split plot design, with inoculum versus no inoculum

as the main plots and three irrigation regimes as subplots. In one treatment, water was applied to the furrows for 4–8 hr once every 14 days (normal irrigation). In a second treatment, irrigations were done on the same 14-day schedule, but alternate irrigations were extended to maintain water in the furrows for at least 24 hr to more fully saturate the beds (prolonged irrigation). In the third treatment, alternate irrigations were withheld, and water was applied to furrows for 4–8 hr once every 28 days (less frequent irrigation). Each treatment was replicated four times.

**Data collection.** The incidence and severity of disease symptoms on shoots of all plants were assessed every other week throughout the growing seasons. Disease symptoms in individual plants were rated on a scale from 0 to 4 (0 = no foliar symptoms; 1 = moderate wilting of foliage; 2 = severe foliar wilting and chlorosis of more than 25% of the foliage; 3 = wilting of main stem, 25–75% of foliage necrotic, 4 = greater than 75% of foliage necrotic, main stem necrotic).

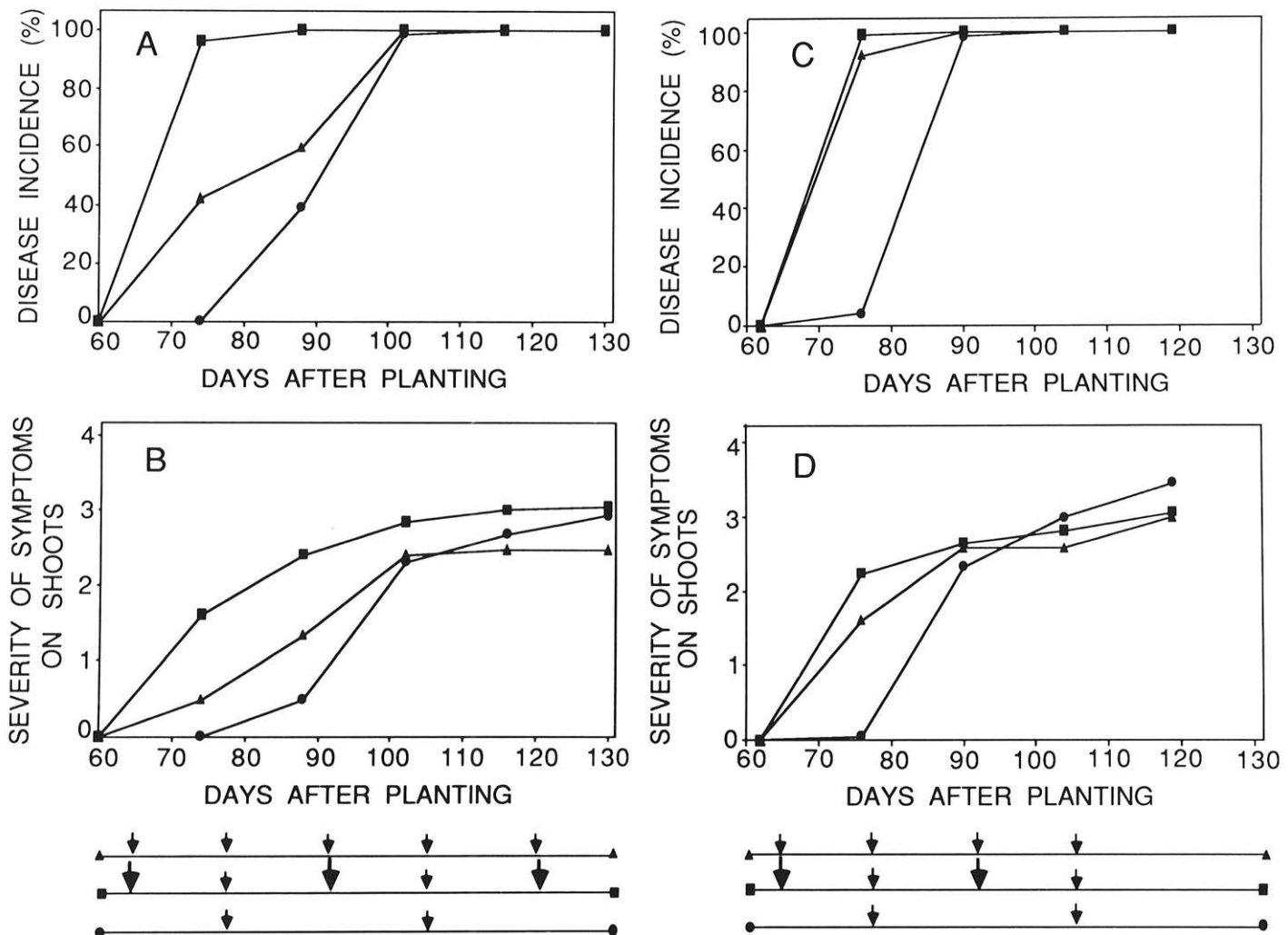
Pre-dawn and midday leaf water potentials ( $\psi_l$ ) were measured before each irrigation with a pressure chamber (Model 3005, Soil Moisture Equipment Co., Santa Barbara, CA). The youngest fully expanded leaflet from each of four randomly selected plants in each experimental unit was used for the measurements, which required a period of 3 hr to complete. The duration of saturated soil conditions in the beds immediately after each irrigation was monitored with tensiometers fitted with mercury manometers in 1986. Tensiometer cups were placed in soil at a depth of 20 cm in the center of one plot of each of the six treatments. Soil

temperature at 20 cm below plant rows was recorded hourly with thermistors (Datapod Digital Recorder DP 222, Omnidata International, Logan, UT).

At harvest, fresh weights of red, green, and rotten fruit were measured. A subset of 15 plants in each plot was evaluated for root rot severity in the top 30 cm of the root zone on a scale of 0–4 (0 = no root discoloration; 1 = less than 25% of all lateral roots brown, no taproot browning; 2 = 26–50% of all lateral roots brown, less than 50% of taproot brown; 3 = 51–75% of all lateral roots brown, 51–75% of taproot brown; 4 = greater than 75% of all lateral and taproots brown). The fungus was isolated from roots in each plot by plating on cornmeal agar amended with pimarin, vancomycin, and PCNB (27).

**Quantification of inoculum in soil.** Soil in each plot was sampled weekly starting immediately after infestation in 1986 to measure population levels of the pathogen. Five soil cores (1.9 cm in diameter and 30 cm deep) were sampled randomly approximately 15 cm from either side of the plant row. The top 10 cm of each core was discarded, and the remaining soil was bulked into a single composite sample per plot. Samples were mixed thoroughly, and all soils were assayed within 24 hr by dilution plating.

Four separate 1:10 dilutions (20 g of soil to 180 ml of 0.25% water agar) were made from each composite sample. From each of the four dilutions, 1-ml samples were spread onto each of five plates of Masago's medium (20) amended with 20  $\mu\text{g/ml}$  of Hymexazol (tachigaren, Sankyo Co., Ltd., Tokyo, Japan). Plates were incubated for 48 hr at 25 C, rinsed with water, and colonies of



**Fig. 1.** Progression of *Phytophthora* root rot on processing tomatoes in inoculated plots: **A**, disease incidence and, **B**, severity of symptoms on shoots (relative scale of 0–4) plotted as a function of days after planting in 1985; **C**, disease incidence and, **D**, severity of symptoms on shoots (relative scale of 0–4) plotted as a function of days after planting in 1986. Irrigation treatments were 4–8-hr irrigations at 14 (triangles) or 28 days (circles), or alternating 4–8-hr and 24-hr irrigations at 14 days (squares). Heavy arrows beneath graph indicate times of 24-hr irrigations and light arrows indicate times of 4–8-hr irrigations.

*P. parasitica* were counted. Moisture content of soil samples was measured gravimetrically, and data were transformed to numbers of colony-forming units per gram (cfu/g) of dry soil.

**Statistical analysis.** Data were tested for normality and homogeneity of variance before analysis of variance with Statistical Analysis System packages (SAS Institute, Inc., Cary, NC). Analysis of variance procedures were conducted by time and a repeated-measures ANOVA also was conducted. Treatment sums of squares were partitioned into single degree of freedom orthogonal contrasts and LSDs were conducted when appropriate. SAS general linear models procedure was used for regression analysis. Percentage data were transformed to arcsins before analysis.

## RESULTS

Prolonged irrigation of inoculated plots caused an increase in disease development relative to that in other treatments in 1985 (Fig. 1A and B). Many plants began to wilt and showed obvious symptoms of disease within 8 days after the first prolonged irrigation, whereas disease severity increased more slowly in plants given normal, 4–8-hr irrigations at 14-day intervals. Disease incidence in inoculated plots given prolonged irrigation was significantly greater than in inoculated plots given less frequent irrigations at 77 days after planting in 1985 (Fig. 1A) and 1986 (Fig. 1C). In 1986, although disease incidence approached 100% 2 wk after the first prolonged and normal irrigations were applied (Fig. 1C), disease severity increased somewhat more rapidly after the prolonged irrigation (Fig. 1D). In both years, the onset of severe disease was delayed in plants that were irrigated on the 28-day schedule, and disease was significantly less in this treatment as compared with other inoculated plots at 77 days after planting. After the first 4-hr irrigation was applied 77 days after planting in the less frequently irrigated plots, disease began to increase rapidly (Fig. 1). Disease severities in plants on the less frequent irrigation schedule, however, finally became as high as (Fig. 1B), or significantly higher (Fig. 1D, 119 days after planting) than those in plants irrigated on the 14-day schedule. Analysis of variance of the disease progress data by time indicated that the inoculation  $\times$  irrigation interaction was highly significant ( $P \leq 0.0001$ ) at each disease measurement time after the first prolonged irrigation in both years. The inoculation main effect was highly significant ( $P \leq 0.0001$ ) at all times. The inoculation  $\times$  irrigation  $\times$  time interaction also was highly significant in both years for both disease incidence and severity data. No perceptible disease developed in plants in uninoculated plots, regardless of irrigation schedule (data not shown).

Analysis of the frequency of occurrence of plants in the different disease severity classes indicated that a majority of plants became infected after the first irrigation in 1986 (Fig. 1C). Disease in the infected plants then became progressively more severe as the season progressed (Fig. 1D). Although fewer numbers of plants became infected after the first normal irrigation in 1985, disease incidence rose rapidly (Fig. 1A). As the season progressed, the increase in mean disease severity (Fig. 1B) resulted more from disease progression in initially infected plants than from increases in numbers of plants infected, i.e., numbers of individual plants with low severity ratings diminished as numbers of individual plants with higher severity ratings increased over time.

Tensiometer measurements of soil  $\psi_m$  after the first differential irrigation episode in 1986 indicated that soil  $\psi_m$  values at a 20-cm depth in the center of the beds were higher for longer periods of time with prolonged than with normal irrigation (Fig. 2). Treatment differences in  $\psi_m$  followed similar trends but were larger in 1985 (data not shown). Mean daily soil temperatures measured at 20-cm depths ranged from 22 to 27 C over the season. Highest soil temperatures were measured early in the season when plant canopies were small.

As symptoms developed in 1986,  $\psi_1$  values in diseased plants decreased. Inoculated plants that received either prolonged or normal 4–8-hr irrigations every 14 days had significantly lower ( $P \leq 0.0001$ ) midday  $\psi_1$  values 76 days after planting than inoculated plants receiving less frequent irrigations (Fig. 3A). Low

midday values were first measured among diseased plants irrigated on the 28-day schedule 90 days after planting and, although their midday  $\psi_1$  remained above  $-10$  bars, these values were significantly lower than in uninoculated control plants. Plants in uninfested plots maintained uniformly high midday  $\psi_1$  regardless of irrigation

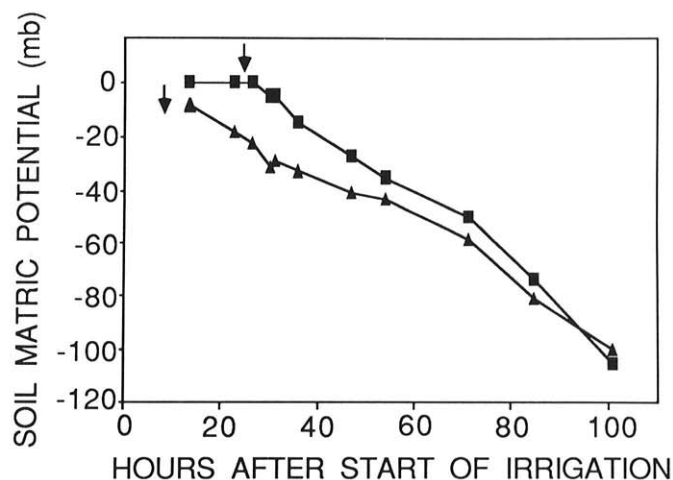


Fig. 2. Soil matrix potentials measured at various times after the first differential irrigation was applied at 63 days after planting in 1986: prolonged, 24-hr irrigation (squares); and the normal, 4–8-hr irrigation (triangles). Tensiometers were 20 cm deep in the center of the bed. Arrows indicate time when water supply to furrows was turned off.

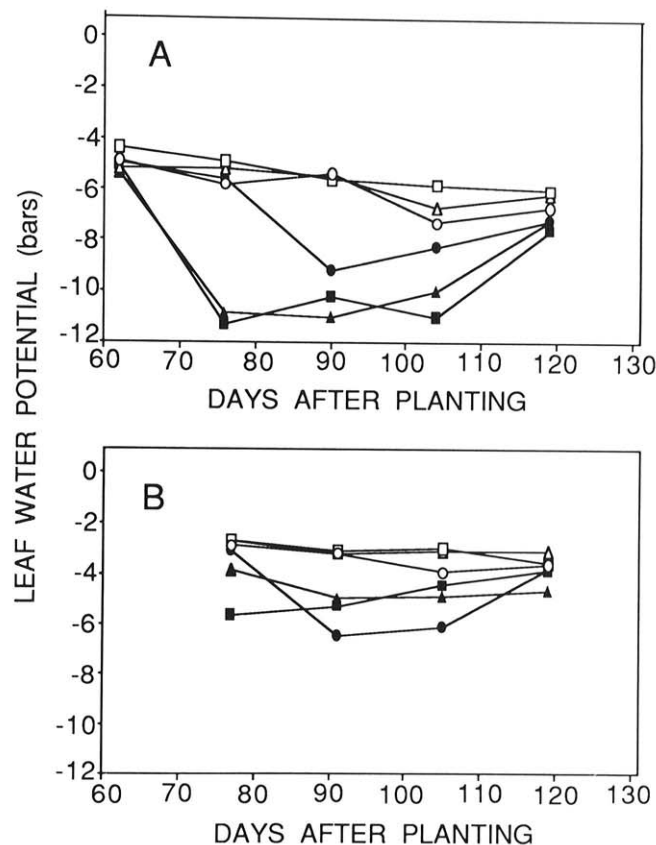


Fig. 3. Leaf water potential ( $\psi_1$ ) of diseased (closed symbols) and healthy (open symbols) tomato plants measured at various times after planting in 1986: **A**, midday; **B**, predawn. Irrigation treatments were 4–8-hr irrigations at 14 days (triangles), or 28 days (circles), or alternating 4–8-hr and 24-hr irrigations at 14 days (squares). LSD<sub>0.05</sub> values of  $P \leq 0.05$  for comparison of midday or predawn  $\psi_1$  treatment means within inoculum levels were 0.68, 1.23, 0.98, 0.94, and 1.02, 1.59, 1.4, and 0.75, respectively, at 76, 90, 104, and 119 days after planting.



TABLE 1. Influence of irrigation schedule and inoculation with *Phytophthora parasitica* on yield of red fruit of processing tomatoes

Irrigation schedule		1985				1986			
		Final disease symptoms on roots <sup>a</sup>		Yield of harvestable red fruit (kg/plot) <sup>b</sup>		Final disease symptoms on roots <sup>a</sup>		Yield of harvestable red fruit (kg/plot) <sup>b</sup>	
		Not Inoculated	Inoculated	Not Inoculated	Inoculated	Not Inoculated	Inoculated	Not Inoculated	Inoculated
Frequency (days)	Duration (hr)								
28	4-8	1.2	2.1	171.2	136.9	0.1	3.3	158.2	91.3
14	4-8	1.1	2.2	199.9	131.4	0.1	3.0	192.4	77.1
14	Alternate 4-8/24	1.1	3.0	200.6	64.4	0.1	3.2	191.6	50.4

<sup>a</sup> Mean root symptom severity (relative scale of 0-4) of inoculated plants all significantly different from uninoculated plants at  $P \leq 0.001$ ;  $LSD_{0.05} = 0.69$  and  $0.34$  for 1985 and 1986, respectively. For comparisons of means within a column,  $LSD_{0.05} = 0.77$  and  $0.34$  for 1985 and 1986, respectively.

<sup>b</sup> Yield data are kilograms fresh weight per 12.2- or 13.7-m length of single-row beds in 1985 and 1986, respectively. For comparison of means between inoculated and uninoculated plots,  $LSD_{0.05} = 48.3$  and  $40.4$  for 1985 and 1986, respectively. For comparisons of means within a column,  $LSD_{0.05} = 44.4$  and  $31.1$  for 1985 and 1986, respectively.

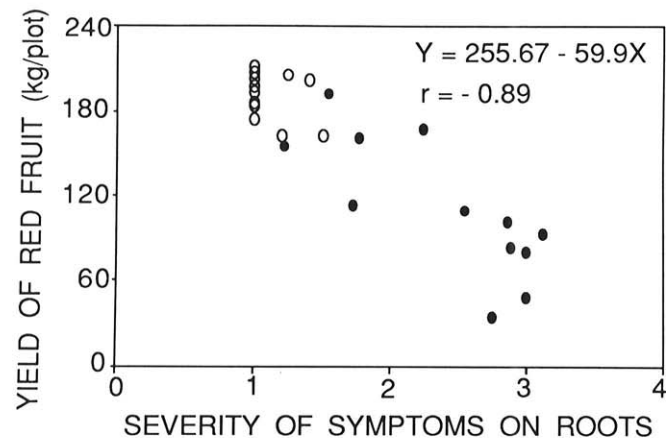


Fig. 4. Red fruit yield at harvest plotted as a function of final severity (relative scale of 0-4) of symptoms on roots for 1985. Uninfested and infested plots are represented by open and closed symbols, respectively. The correlation coefficient from linear regression analysis was significant at  $P \leq 0.0001$ .

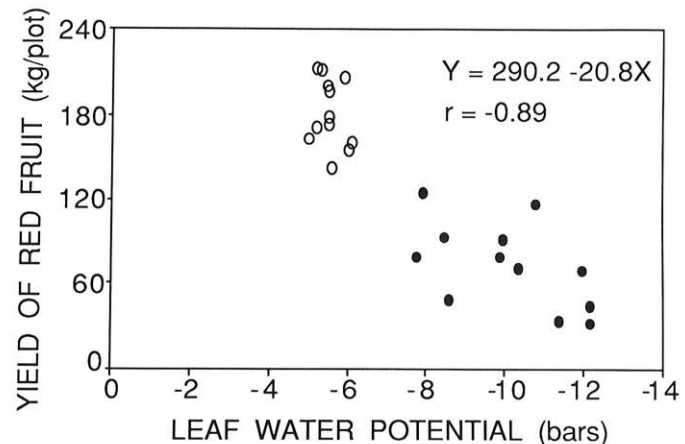


Fig. 5. Red fruit yield at harvest plotted as a function of midday leaf water potential measured 90 days after planting in 1986. Uninfested and infested plots are represented by open and closed symbols, respectively. The correlation coefficient from linear regression analysis was significant at  $P \leq 0.0001$ .

TABLE 2. Regression analyses relating final yield of red fruit to leaf water potential ( $\psi_1$ ) measured midday at various times during the 1986 season

Days after planting	Regression equation relating yield to $\psi_1^a$	$r^2$
62	$Y = 234.4 - 21.5 X$	0.06
76	$Y = 252.6 - 17.3 X$	0.65 <sup>b</sup>
90	$Y = 290.2 - 20.9 X$	0.80 <sup>b</sup>
104	$Y = 341.9 - 26.3 X$	0.78 <sup>b</sup>
119	$Y = 399.8 - 40.1 X$	0.39 <sup>b</sup>

<sup>a</sup> Data used were from all experimental units where  $X$  is the average  $\psi_1$  and  $Y$  is the yield of red fruit.

<sup>b</sup> Coefficient of determination significant at  $P \leq 0.001$ .

inoculated plants than at previous measurement times (Fig. 3). This apparent recovery in  $\psi_1$  was due to regrowth of infected plants at the end of the season. Only fresh green leaves were usable in the pressure chamber, and their  $\psi_1$  values were finally higher than the average for diseased plants.

Although aboveground symptoms of disease finally became severe in the infested plots of all irrigation treatments, irrigation had large effects on final severity of symptoms on roots and yield of treatment (Fig. 3A). During the same time period, predawn  $\psi_1$  was uniformly lower in inoculated than in uninoculated plants, and the inoculum effect was significant (Fig. 3B). By 119 days after planting, both predawn and midday  $\psi_1$  values were higher in diseased plants (Table 1). Analysis of variance of the total and red fruit yields from 1985 and 1986 revealed significant ( $P \leq 0.01$ ) effects of inoculation and the inoculation  $\times$  irrigation interaction. In uninfested plots, an increase in irrigation frequency had a

positive effect on yield, whereas in infested plots an increase in the frequency and duration of irrigation had a negative effect on yield (Table 1). Although yields from infested plots were lower in 1986, treatment effects on total and red fruit yield followed similar trends in both years (Table 1). Disease reduced the yield of plants that received prolonged irrigations by 68 or 74% as compared with uninfested controls in 1985 or 1986, respectively. Yield reductions due to disease in treatments that received 4-8-hr irrigations at 14- and 28-day intervals were 34 or 60% and 20 or 43% in 1985 or 1986, respectively. A highly significant negative and linear relationship existed between severity of root rot at harvest and final yield of red fruit (Fig. 4).

Regression analyses, with midday  $\psi_1$  measured at various times during the 1986 season as the independent variable and final yield of red fruit as the dependent variable, revealed that final yield was related linearly to midday  $\psi_1$  during some periods of disease development (Table 2). Midday  $\psi_1$  values ranged from -4 to -6 bars at 62 days after planting and were not related to yield. By 90 days after planting, when symptom expression was near its maximum, a significant negative and linear relationship was found between midday and red fruit yield (Fig. 5, Table 2). Significant negative and linear relationships also were found between midday  $\psi_1$  and red fruit yield at 76, 104, and 119 days after planting (Table 2), but coefficients of determination were lower than at 90 days after planting. Random scatter of plots of the residual error terms indicated that the linear models were a good fit to the data.

In artificially infested plots, population densities of *P. parasitica* in 1986 ranged from 6 to 17 cfu/g of soil immediately after infestation (Fig. 6). *P. parasitica* was not recovered from uninfested plots. Population densities increased in all infested plots after the first uniform irrigation applied 44 days after planting.

After the initial increase at 62 days after planting, populations in infested plots varied greatly with time in a cyclic pattern that was not always synchronous for all irrigation treatments. The highest population densities were found in the normal 4–8-hr, 14-day irrigation schedule. At the end of the season, plots irrigated on the 28-day schedule had 67 cfu/g (range 52–83) of soil, whereas plots given the prolonged or normal irrigation regime had 103 cfu/g (range 29–245) and 121 cfu/g (range 26–267) of soil, respectively.

## DISCUSSION

Irrigation frequency and duration had large effects on disease progress and final yield in infested plots. Significantly greater amounts of disease developed early in the season in inoculated plants given prolonged irrigations, and the onset of disease symptoms was delayed in plants irrigated less frequently on the 28-day schedule (Fig. 1). The fact that aboveground symptoms in both years were delayed until after the first 4–8-hr irrigation suggests that irrigation had large effects on disease initiation. Further, because the time of disease development was influenced by irrigation schedule, subsequent yield of disease plants also was affected by irrigation regime (Table 1). Greatest yield reductions were found in inoculated plants given more frequent and prolonged irrigations, whereas yield reductions in less frequently irrigated, infested plots were not as large due to the delay in disease onset.

Rates of increase in root disease caused by some other soilborne *Phytophthora* spp. have been measured quantitatively in the field (7,11). Ferrin et al (11) showed that cyclic increases in soil water status resulted in cyclic increase in plant mortality in a tobacco cultivar susceptible to *P. parasitica* var. *nicotianae*. Although their soil  $\psi_m$  data do not reflect all fluctuations in soil moisture, the work showed a clear relationship between increased plant mortality and increased soil moisture under field conditions.

Disease progress curves for black shank caused by *P. p. nicotianae* on several tobacco cultivars showed a gradual increase in disease incidence over a period of several months (7,11). Our disease progress curves demonstrated a more rapid increase in disease that occurred after irrigations (Fig. 1). These rapid increases in disease incidence probably were due partly to the high population densities and uniform distribution of inoculum in the experimental units of our study. Many roots probably grew in close proximity to or contacted inoculum early in the season, facilitating 100% disease incidence under prolonged irrigation. Further, the application of irrigation water to soil, especially prolonged irrigation, caused a rapid shift to conditions that probably were conducive for zoospore formation, release, and dispersal (10). Whereas both biological and statistical models have

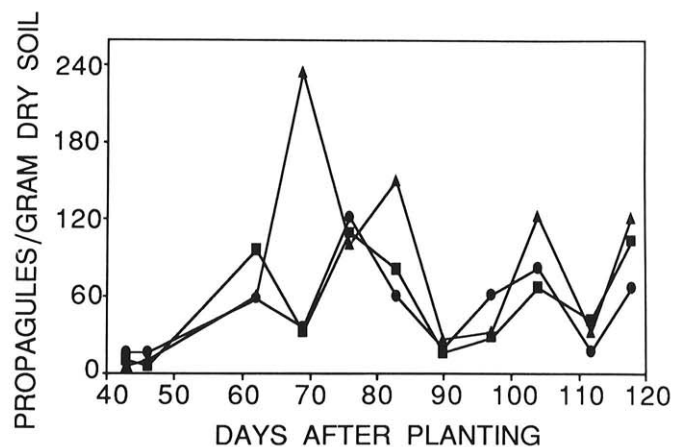


Fig. 6. Population densities of *Phytophthora parasitica* in infested soil in the 1986 field site determined by a soil dilution plate assay. Each point represents the mean from four plots. Irrigation treatments were 4–8-hr irrigations at 14 (triangles) or 28 days (circles), or alternating 4–8-hr and 24-hr irrigations at 14 days (squares).

been used to describe the kinetics of root diseases (6), previous transformations and models were not used to describe the rapid increase in disease incidence reported here for *Phytophthora* root rot of tomato (Fig. 1). Studies with *Aphanomyces* root rot of pea have demonstrated that disease incidence increases rapidly early in the season at high inoculum densities, which shorten the length of time required to reach 50% disease incidence (21).

Measurements of soil  $\psi_m$  after the differential irrigation applied 63 days after planting in 1986 (Fig. 2) demonstrated that the duration of time soil  $\psi_m$  values were above  $-20$  mb was longer following a 24-hr than a 4–8-hr irrigation. Soil  $\psi_m$  values required for infection are similar to those required for zoospore release and dispersal in a number of *Phytophthora* spp. (26). In fact, zoospore release is extremely sensitive to changes in soil  $\psi_m$ , and is inhibited at  $\psi_m$  below  $-25$  mb in several *Phytophthora* spp. (10). Therefore, conditions probably were conducive for zoospore release and dispersal to roots for longer periods after 24-hr irrigations, which may explain why prolonged irrigations accelerated disease development early in the season. Likewise, a delay in disease with less frequent irrigation may be expected, since conditions were conducive for zoospore release and dispersal less often in this treatment. Even though the soils at both field sites were clay loams, the field used in 1986 was less well-drained than the field used in 1985. Tensiometer data indicated that beds in the normal irrigation treatment were wetted more extensively and for longer periods in 1986 than in 1985. This difference in soil moisture may have accelerated disease development in 1986 relative to that in 1985 (Fig. 2). In addition, other differences between years, including soil temperatures, may have affected disease progress.

*Phytophthora* root rots are potentially multicyclic diseases (7,10,11), with cycles of both inoculum production and spread from plant-to-plant during the growing season. As reported for other *Phytophthora* spp. (12,17,24), we found cyclical increases and decreases in pathogen population density in soil during the growing season. Population densities of *P. parasitica* observed in tomato field soil fluctuated widely but showed net increases from 6–17 to 67–121 cfu/g of soil during the growing season. Multiple cycles of sporangium formation, zoospore release, and infection probably occurred with each irrigation in our study. Populations of *P. p. nicotianae* increased from 0.75 to 250 cfu/g of soil in the rhizosphere of susceptible tobacco during the growing season (17). Plant-to-plant spread of *P. p. nicotianae* in tobacco fields was related to the level of host resistance (25). Spread of inoculum between tomato plants in irrigation water probably occurred in our experiments, although actual zoospore populations were not monitored in irrigation water. Hoy et al (13) demonstrated zoospore activity in water in furrow-irrigated tomatoes as early as 1 hr after irrigations began. The role of plant-to-plant spread in development of *Phytophthora* root rot in tomato needs more thorough examination. Apparently, initial infection of many plants after the first irrigation (Fig. 1A) and subsequent increase in disease severity within individual plants contributed more to disease development than did plant-to-plant spread in our experiments. Inoculum dispersal among roots may have affected the rate of disease development in individual plants. However, in naturally infested field soils with lower levels of initial inoculum distributed less evenly, disease progress is more likely to depend on plant-to-plant spread.

Measurements of predawn and midday  $\psi_1$  demonstrated that *Phytophthora* root rot induced water stress in tomato plants (Fig. 3). Predawn  $\psi_1$  was uniformly lower in inoculated than uninoculated plants, indicating that plants did not recover fully from water stress during the night, and that water uptake was affected by disease. Infection of safflower and soybean roots by *Phytophthora* spp. caused marked increases in resistance to water uptake through roots (8,18), and such an effect probably also occurs in tomato. Water stress can have major effects on expansive growth, photosynthesis, and other physiological processes that contribute to fruit yield in plants (14). In our study, depression in midday  $\psi_1$  measured during several stages of growth was a useful indicator of both symptom severity and red fruit yield at harvest (Table 2, Fig. 5). Results suggest that severe water stress induced by

disease during periods of rapid vegetative growth and flower and fruit set can have major impacts on fruit yield. Others have used  $\psi_1$  as an indicator of water stress in tomatoes and related physical stress factors to yield (23). Further, the inverse relationship between yield and final severity of symptoms in larger roots recovered from the top 30 cm of soil suggests that infection of these larger roots is highly detrimental to yield.

Variations in the frequency and duration of furrow irrigation can have large effects on the development of *Phytophthora* root rot in processing tomatoes. In irrigated tomato production areas, there is the potential to manipulate soil water status to reduce *Phytophthora* root rot and the impact of the disease on yield. In areas of fields infested by *P. parasitica*, prolonged or heavy irrigations early in the season may lead to disease increase relative to that which may occur with more brief or moderate irrigations, whereas a delay in disease onset is possible if plants are irrigated less frequently. If severe disease is delayed until after flowering and early fruit set, yield reductions due to the disease will be less severe. In fields infested with *Phytophthora*, the avoidance of prolonged irrigation early in the season and the application of well-timed less frequent irrigations of shorter duration will lead to increased yields. It is clear that soil water is a major parameter in the onset and development of *Phytophthora* root rot, and that better management of the disease will require changes in irrigation practices in infested fields.

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