

Population Densities of *Phytophthora capsici* in Field Soils in Relation to Drip Irrigation, Rainfall, and Disease Incidence

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ABSTRACT

Ristaino, J. B., Hord, M. J., and Gumpertz, M. L. 1992. Population densities of *Phytophthora capsici* in field soils in relation to drip irrigation, rainfall, and disease incidence. *Plant Dis.* 76:1017-1024.

Population dynamics of *Phytophthora capsici* were monitored in artificially infested plots in fields planted with bell peppers (*Capsicum annuum*). Plots were drip-irrigated on either a more frequent (three times per week) or a less frequent (one or two times after infestation) schedule and were infested with one of three levels of inoculum or left uninfested. Pathogen population densities increased and then decreased over time in each field. In a field with moderate rainfall, plots had population densities of 0, 5, 18, and 41 cfu/g of dry soil at the time of infestation. Population densities were higher 41 days after planting in plots irrigated more frequently than in those irrigated less frequently. Population densities early in epidemic development were positively correlated with disease incidence and soil water content at the time of sampling. In the moderate rainfall field, changes in population densities over time were greater on the side of the plots where the drip irrigation line was located than on the opposite side. Population densities in plots of a field with high rainfall were 0, 2, 8, and 38 cfu/g of dry soil at the time of infestation and were not affected significantly by the frequency of irrigation or the location of the drip irrigation line. Population densities in the high rainfall field were highest 42 days after planting following a heavy rainfall early in the season. The pathogen spread into uninfested plots and was detected after symptoms of disease appeared in each field. At the end of the season, the field with high rainfall had higher population densities of *P. capsici* in initially uninfested plots than the field with moderate rainfall. In both fields, population densities in soil were too high to allow determination of a threshold below which disease was negligible, and populations declined when disease incidence was high.

Phytophthora capsici Leonian causes a severe root and crown rot and aerial blight on peppers (*Capsicum annuum* L.) (7,22,24). Irrigation and rainfall can have significant effects on the disease in the field and on pathogen spread (7,8,24,28). Disease onset was earlier and the final incidence of disease was higher in plots drip-irrigated more frequently rather than less frequently when rainfall was low (24). With high rainfall, the total amount of rainfall can have large effects on the rate of disease development, amount of disease spread, areas under the disease progress curve, and subsequent yield in bell pepper (7,24).

Changes in the matric component of soil water potential (ψ_m) can have

significant impacts on the development of *Phytophthora* root rot diseases and on pathogen population densities in soil (9). Mycelial disks of *P. capsici* incubated in saturated soil did not form sporangia under saturated conditions unless first incubated in soil held at ψ_m of -20 to -30 J/kg (5). Saturated soil conditions are also conducive for zoospore release from sporangia and dispersal of inoculum in the field (9). Inoculum density-disease relationships of *Phytophthora* species can be significantly altered by changes in ψ_m (20,24,30). Low levels of inoculum of *P. parasitica* var. *nicotianae* caused large amounts of disease in tobacco in naturally infested soil given a single saturation period in tension funnel experiments (30).

Little is known about the actual population densities of *P. capsici* in infested fields or about factors that affect the dynamics of pathogen populations over time. Naturally infested pepper fields in New Jersey had between two and 24 propagules of *P. capsici* per gram (ppg)

of soil during the season, but propagules were not detectable when fields were sampled before planting (22). Introduced populations of *P. capsici* declined rapidly in soil sampled between plant rows (22). Population densities of *Phytophthora* species in soil are dynamic and can be influenced by soil physical and chemical factors and the presence of actively growing susceptible roots (4,10,25,32).

Oospores are believed to be the primary overwintering propagule in fields infested with *P. capsici* (2,6). However, quantification of initial inoculum densities of *P. capsici* in naturally infested fields has been limited because of the low level of germination of oospores on selective media (15,22). Oospores of *P. capsici* germinate predominantly to form sporangia and release zoospores in soil and root extracts and root exudates (15). Zoospores released from sporangia during periods of soil saturation cause extensive disease in pepper and are probably the primary infective propagule in the field (7,16). Enumeration of propagules of *Phytophthora* species in naturally infested soil with dilution plating techniques has been reported by many workers, and although this technique has limitations, it is currently the method of choice in quantitative studies (10,12,13,17,22,31,33).

Knowledge of the factors that affect populations of *P. capsici* in field soil may help target management strategies to reduce disease caused by the pathogen. In a previous paper (24), the influence of rainfall, drip irrigation, and inoculum density on the disease progress caused by *P. capsici* and the yield of bell pepper was described, but the dynamics of pathogen populations in soil and their relation to disease were not included. The objective of this work was to describe the population dynamics of *P. capsici* in field soil artificially infested with different amounts of inoculum and to evaluate the influence of the frequency of drip irrigation, the location of the drip line, rainfall parameters, and disease incidence on changes in pathogen densities

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Accepted for publication 21 April 1992.

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over time. A portion of this work was published previously (26).

MATERIALS AND METHODS

Inoculum production. One isolate of *P. capsici* (Sc 2A, type A1) pathogenic to pepper was used to infest soil in field plots. Cultures were maintained on cornmeal agar slants or V8 juice agar in petri dishes (800 ml of water, 200 ml of V8 juice, 2 g of CaCO₃, 18 g of agar). Inoculum for use in field experiments was prepared by culturing the fungus at 25 C for 6–7 wk in 500 cm³ of vermiculite and 250 ml of V8 broth in 1-L mason jars. Inoculum consisted of hyphae and sporangia of the fungus.

Preliminary experiments were conducted in the laboratory to determine the percentage of zoospores of *P. capsici* that germinated on three selective media. Zoospores from 13 isolates of *P. capsici* were evaluated for germinability on PARP medium (17), Masago's medium (19), and P₅VPP-BH (22). Masago's medium was selected for quantification of propagule density in soil because colony morphology was distinctive and germination of zoospores was higher than on the other two media. Isolate Sc 2A was chosen because 82–93% of the zoospores plated on Masago's medium germinated and because this isolate was virulent on pepper in greenhouse assays (23).

Field experiments. The pathogen population density data were collected as part of field tests conducted in 1988 and 1989 (24) on a Johns sandy loam soil (63% sand, 28% silt, 9% clay) at the Central Crops Research Station in Clayton, North Carolina, and in 1988 on

an Orangeburg loamy sand soil (87% sand, 8% silt, 5% clay) at the Horticultural Crops Research Station in Clinton, North Carolina. Many of the methods used have been described previously (24). Seedlings (8 wk old) of pepper cv. Keystone Resistant Giant were transplanted 40 cm apart into raised, single-row beds of soil fumigated previously with methyl bromide–chloropicrin (392 kg/ha). Soil was fumigated to eliminate nematodes from the experimental field areas and also because many pepper growers in North Carolina routinely fumigate before transplanting. Experimental units were 12.2 m long and 1.1 m wide. At each site, treatments were arranged in a split-plot design, with irrigation as main plots and levels of inoculum as subplots. The main plots were arranged in four blocks. The ends of adjacent plots were separated with soil berms 30 cm high and unplanted borders 6.1 m long.

Soil in subplots was either left uninfested or infested 43, 35, or 31 days after transplanting (Clayton 1988, Clinton 1988, and Clayton 1989, respectively) with one of three levels of inoculum of *P. capsici* grown on V8 vermiculite medium (24). Soil in plots was infested after transplants were established to avoid immediate loss of plant stands. Inoculum was spread uniformly in a band approximately 20 cm from either side of the plant row and covered with soil to a depth of approximately 10 cm. Care was taken to avoid damage to roots at the time of infestation of soil with the pathogen. Inoculum of *P. capsici* was applied to subplots at the highest level (1.0x) at a rate of 208 cm³/m of row.

Inoculum was diluted 10-fold and 100-fold with uninfested V8 vermiculite medium before incorporation into soil at the same rate to give 0.1x and 0.01x levels of inoculum. Soil in control plots was not infested and did not contain detectable inoculum of the pathogen at the first soil sampling date.

Irrigations were applied to main plots with a drip system. A single drip irrigation line (Typhoon 20, Netafim Irrigation Inc., Valley Stream, NY) with in-line emitters spaced 40 cm apart was buried 10 cm below the soil surface and approximately 10 cm from one side of the plant row in each plot. Plots were either irrigated less frequently (only after soil infestation with the pathogen or to avoid water stress) or more frequently (three times per week for 4 hr each time). Plots were not irrigated on days when rainfall occurred. Water was applied at a rate of 1.9 L/min/30.5 m of row at a pressure of 68.9 J/kg. All plots in the Clayton field area were drip-irrigated uniformly for 4 hr either 1 or 3 days after infestation with the pathogen in 1988 and 1989. Rainfall occurred within 2 days after infestation of the plots in the Clinton field in 1988.

Measurement of inoculum densities, soil water content, and disease. Soil from three replicates of each treatment was sampled immediately after infestation and four times during the season to estimate population densities of *P. capsici* over time. Fifteen cores (1.9 cm diameter × 20 cm deep) were sampled from each side of the plot in a straight line approximately 20 cm from the plant row. The top 5 cm of soil from each core was discarded, and cores were combined into two composite samples for either the drip irrigation side or the opposite side of the plant row. Soil was placed in plastic bags, held at room temperature, and assayed within 2 days of sampling. Three subsamples of soil were removed from each composite sample, and three separate dilutions were made from each soil sample with 0.25% water agar. Soil from plots infested with the highest level of inoculum (1.0x) was diluted 1:10 (w/v), whereas soil from uninfested plots and plots infested with the medium level of inoculum (0.1x) was diluted 1:5 and soil from plots infested with the lowest level of inoculum (0.01x) was diluted 1:2. From each dilution, a 1-ml sample was spread onto Masago's medium (19) amended with hymexazol at 20 µg/ml (99.5% a.i. Tachigaren) in each of five petri dishes. After incubation at 25 C in the dark for 48–72 hr, dishes were rinsed with water and colonies of *P. capsici* were counted. Inoculum density was defined as the number of colony-forming units per gram of dry soil.

The incidence of disease on shoots was evaluated visually during the growing season. Disease was evaluated at more frequent intervals during phases of rapid

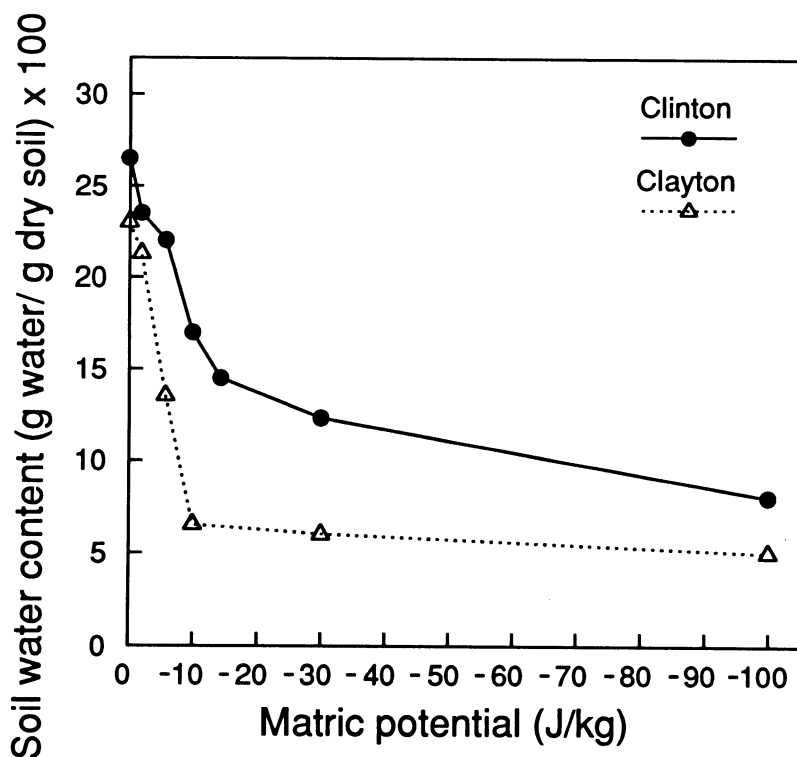


Fig. 1. Soil moisture release curve for field soils at two locations in North Carolina.

epidemic development. Plants were considered diseased when a black lesion was visible on the main stem or crown of the plant. Plant tissue from the crown and roots was sampled periodically, surface-disinfested, and plated on a selective medium (17) to reisolate the pathogen and confirm that infections were caused by *P. capsici*.

Rainfall data were recorded with rain gauges located near the plots on each research station. Soil water content in each plot was measured gravimetrically from three subsamples at the time that soil was assayed for populations of *P. capsici*. A soil moisture release curve (Fig. 1) was determined for sieved (10-mm mesh) soil at ψ_m values between 0 and -100.0 J/kg with either Büchner tension funnels or a pressure plate. The sandy loam soil at the Clinton field retained a greater percentage of water at each ψ_m measured than the loamy sand soil at the Clayton field (Fig. 1). The soil moisture release curve is included so that soil water contents can be converted to ψ_m in the figures presented.

Data analysis. Data were tested for homogeneity of variance before analysis of variance with the Statistical Analysis System (SAS Institute, Cary, NC). Sample means were proportional to their standard deviations, so pathogen population density data were transformed with the $\log_{10}(x + 1)$ transformation, where x = the number of colony-forming units per gram of dry soil. Multivariate repeated measures analysis of variance was conducted on transformed pathogen population density data and soil water content data with the repeated measures option of the SAS General Linear Models procedure because dependent variables were serially correlated (14). Levels of irrigation were specified in the model as main plots, inoculum levels were specified as subplots, and sides of the bed from which samples were removed (at drip line vs. opposite drip line) were specified as sub-subplots. The appropriate error terms were used to test all main plot, subplot, and sub-subplot effects. Tests of the effect of time and time \times treatment interactions were performed using Wilks's lambda, which is a likelihood ratio test statistic for multivariate analysis of variance (14). Because results from the experiments conducted in the low and moderate rainfall fields in Clayton in 1988 and 1989 were similar, data from the moderate rainfall field in 1989 are shown and compared with data from the high rainfall field in Clinton in 1988.

Rain variables were calculated with the total daily centimeters of rainfall at each location. The number of days in the period was determined by calculating the time interval in days between pathogen population sampling dates. The total centimeters of rainfall were calculated as the sum of the daily centimeters of

rainfall in a period. The rate of rainfall (cm/day), the intensity of rainfall (cm/rain day), and the proportion of days with rainfall >2.0 cm in the period were calculated.

Data were sorted by irrigation level, and correlation analysis was conducted on the transformed pathogen density,

rain variables, soil water content, and disease incidence data. In addition, data were sorted by time period and irrigation level, and correlation analysis was conducted on the disease incidence, soil water content, and transformed pathogen density data. Not all disease incidence data were used in the correlation

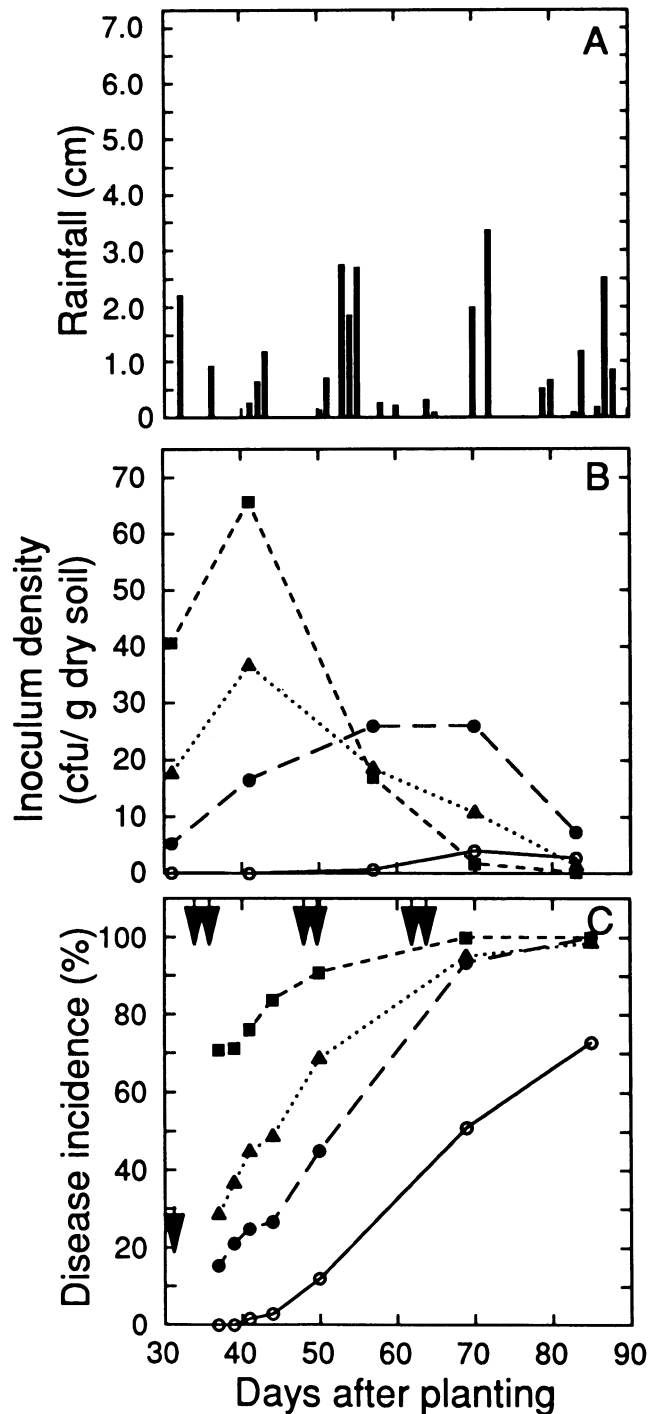


Fig. 2. Total rainfall distribution and progression of *Phytophthora* root rot in bell peppers in plots infested with *P. capsici* at the moderate rainfall field in Clayton in 1989: (A) Total rainfall distribution. (B) Population densities of *P. capsici* over time in plots uninfested (O) or infested at one of three levels of inoculum (● = 0.01x, ▲ = 0.1x, ■ = 1.0x). Inoculum main effect means are shown over time. (C) Disease incidence over time in plots uninfested (O) or infested at one of three levels of inoculum (● = 0.01x, ▲ = 0.1x, ■ = 1.0x) applied 31 days after transplanting. Disease main effect means are shown over time. Top arrows indicate times of application of drip irrigations, and bottom arrow indicates time of infestation with *P. capsici*.

analysis because disease incidence was monitored more frequently than pathogen density in soil.

RESULTS

Population dynamics at the moderate rainfall field in Clayton in 1989. Approximately 22 cm of rain occurred at the moderate rainfall field in Clayton in 1989 (Fig. 2A). A 2.2-cm rain event occurred 1 day after the plots were infested, and propagule densities increased in all infested plots (Fig. 2B). Pathogen densities in soil were not correlated with the other rain events that occurred later in the season (Fig. 2B).

Pathogen population densities at the time of infestation of the plots at 31 days after planting (DAP) were 0, 5, 18, and 41 cfu/g of dry soil at the 0, 0.01x, 0.1x, and 1.0x inoculum levels, respectively (Fig. 2B). Highest propagule densities occurred early in epidemic development in plots infested with the 1.0x and 0.1x levels of inoculum, as observed at 41 DAP. Changes in propagule densities over time were significantly different (time × inoculum effect significant at $P < 0.01$) between all levels of inoculum in infested plots (Fig. 2B, Table 1). *P. capsici* was detected in initially uninfested plots at 57 DAP, and population densities increased slightly with time to 3 cfu/g by the end of the season (Fig. 2B).

Disease increased rapidly in all infested plots after a heavy rainfall that occurred at 32 DAP (Fig. 2C). The rate of disease increase over time was affected

by inoculum level (time × inoculum significant at $P < 0.01$), but the frequency of irrigation did not affect disease increase over time (Fig. 2C). There was a significant positive correlation between inoculum density and disease incidence at 41 DAP ($r = 0.56$ at $P < 0.01$). However, the final incidence of disease in all initially infested plots reached 100% by the end of the season and was independent of the level of inoculum applied to plots (Fig. 2C). *P. capsici* was detected in initially uninfested plots at 56 DAP (Fig. 2B), whereas aboveground symptoms of disease were detected at 41 DAP (Fig. 2C). Final incidence of disease in initially uninfested plots was 73% (Fig. 2C).

Although the frequency of irrigation did not affect disease increase, irrigation frequency had a significant effect on pathogen population densities over time (Fig. 3A, Table 1). Highest propagule densities in infested plots were measured at 41 DAP and were 46.7 and 32.5 cfu/g of dry soil in plots irrigated more frequently or less frequently, respectively.

The changes in pathogen densities of *P. capsici* over time were also significantly affected by the side (time × side effect significant at $P < 0.01$) of the plot where the drip irrigation line was located (Fig. 3B, Table 1). Because irrigation levels were assigned to main plots, more precise comparisons could be made between sides of a plot than between irrigation levels. Highest propagule densities in infested plots were measured at 41 DAP, and propagule densities were

40.1 cfu/g of dry soil on the drip irrigation line side and 20.9 cfu/g of dry soil on the opposite side of the plots. Soil water content over time was greater (time × irrigation × side effect significant at $P < 0.01$) in plots irrigated more frequently on the side of the plots where the drip irrigation line was located than on the opposite side of plots or in plots irrigated less frequently (Fig. 3C). Consequently, side was a better indicator of the amount of water received in the plots than the nominal irrigation level. The largest differences in soil water content between these plots occurred at 41 DAP (Fig. 3C) and corresponded to the time when differences in pathogen population densities were largest among treatments (Fig. 3B). Soil water content at 41 DAP was correlated positively with population densities ($r = 0.34$ at $P = 0.05$). Soil water content changed with time in the plots and was not different between treatments later in the season (Fig. 3C) after several heavy rainfalls (Fig. 2A). Soil water content was not correlated with population densities later in the season. In plots irrigated less frequently, soil water content was positively correlated with the rate of rainfall ($r = 0.200$ at $P = 0.05$).

Population dynamics at the high rainfall field in Clinton in 1988. More rainfall (31 cm) occurred at the Clinton field in 1988 (Fig. 4A) than at the Clayton field in 1989 (Fig. 2A). Soil was infested with the pathogen at 35 DAP, and a 6.0-cm rainfall occurred 2 days after the plots were infested (Fig. 4A). Pathogen population densities were highest at 42 DAP in plots infested with the 1.0x (37 cfu/g) and 0.1x (34 cfu/g) levels of inoculum, decreased with time, and did not increase in these plots after other rainfalls later in the season (Fig. 4B).

Population densities were 0, 2, 8, and 38 cfu/g of dry soil at the first sampling time at 35 DAP (Fig. 4B, Table 1). Changes in population densities over time were significantly different between plots infested with the 1.0x level and the 0.01x level of inoculum (Fig. 4B, Table 1). *P. capsici* was detected in initially uninfested plots at 55 DAP and increased to 18 cfu/g of dry soil by the last sampling date (Fig. 4B). Changes in pathogen densities over time were significantly different between initially uninfested plots and plots infested at the 0.1x or 1.0x levels of inoculum (Table 1, Fig. 4B).

Disease increased rapidly in all infested plots after the 6.0-cm rainfall that occurred at 37 DAP, and irrigation frequency did not affect the time of disease onset or the final incidence of disease (Fig. 4C). The final incidence of disease was independent of inoculum levels added to plots. The final incidence of disease reached high levels in all plots by 83 DAP (Fig. 4C). Plants in initially uninfested plots showed symptoms of disease at 42 DAP (Fig. 4C), before detectable levels of pathogen were mea-

Table 1. Repeated measures analysis of variance of the effect over time of inoculum level, drip irrigation, and location of the drip irrigation line on the population densities of *Phytophthora capsici* added to field soil at two locations

Source of variation ^a	P values ^b	
	Clayton 1989	Clinton 1988
Time	0.05*	0.62
Time × irrigation ^c	0.05*	0.14
Time × inoculum ^d	0.01**	0.01**
Time × 1x vs. 0.1x	0.01**	0.17
Time × 1x vs. 0.01x	0.01**	0.01**
Time × 0.1x vs. 0.01x	0.04*	0.09
Time × 0 vs. 0.01x	0.01**	0.12
Time × 0 vs. 0.1x	0.02*	0.01**
Time × 0 vs. 1.0x	0.01**	0.01**
Time × irrigation × inoculum	0.13	0.36
Time × side ^e	0.01**	0.08
Time × irrigation × side	0.15	0.51
Time × inoculum × side	0.28	0.59
Time × irrigation × inoculum × side	0.46	0.14

^aThe time effect was tested with time × rep as an error term, the time × irrigation interaction effect was tested using time × irrigation × rep as an error term, and the time × inoculum and time × irrigation × inoculum interaction effects were tested using time × irrigation × inoculum × rep as an error term in the analysis of variance.

^bThe probabilities resulting from tests with Wilks's lambda, a likelihood ratio test statistic (14); * = significance at the 0.05 level, ** = significance at the 0.01 level.

^cDrip irrigations were applied to main plots on a more frequent or a less frequent schedule for 4 hr.

^dInoculum of *P. capsici* was applied in V8 vermiculite to subplots at one of four levels (0, 0.01x, 0.1x, or 1.0x) at a rate of 208 cm³/m of row.

^eFifteen soil cores were removed from each plot approximately 20 cm from either the drip irrigation side or the opposite side of the plant row. A composite sample for each side of the plot was used for soil dilutions on selective medium.

sured in soil in these plots (Fig. 4B). Disease incidence reached 85% at the end of the season in initially uninfested plots (Fig. 4C).

In contrast to findings in the moderate rainfall field (Fig. 3A), changes in pathogen population densities over time in the high rainfall field were not affected by the frequency of irrigation (Fig. 5A, Table 1). However, the rate of decrease in pathogen population densities in infested plots between 42 and 55 DAP was significantly greater in plots irrigated more frequently than in those irrigated less frequently (irrigation effect significant for the rate of decrease in pathogen density between 42 and 55 DAP at $P < 0.05$).

Also, in contrast to findings in the moderate rainfall field (Fig. 3B), changes in pathogen densities over time were not significantly affected by the location of the drip irrigation line (Fig. 5B, Table 1). Soil water contents differed over time in plots irrigated more frequently and were greater on the side of the plot where the drip irrigation line was located than on the opposite side of plots or in plots irrigated less frequently (time \times irrigation \times side effect significant at $P < 0.01$). Differences in soil water content between treatments were largest at 42 and 69 DAP (Fig. 5C). Soil water contents were similar in all plots at the last sampling time (Fig. 5C) because of multiple rainfall events late in the season (Fig. 4A). Soil water contents in plots irrigated either more or less frequently were positively correlated with the rate of rainfall ($r = 0.42$ and 0.24 at $P < 0.01$ and 0.01 , respectively) and all of the other rain variables calculated.

DISCUSSION

In a field with moderate rainfall, population densities of introduced inoculum of *P. capsici* in soil increased to a greater extent in plots irrigated more frequently than in those irrigated less frequently early in epidemic development. The largest increases in population densities over time due to more frequent drip irrigation occurred in the moderate rainfall field at Clayton in 1988. Lutz and Menge (18) reported increases in population densities of *P. parasitica* from 17 ppg of soil the day before an irrigation to 70 ppg of soil 2 days after long-interval furrow irrigation in citrus soils in California. In addition, population densities of *P. parasitica* were significantly greater under furrow than drip irrigation in citrus soils because furrow irrigation saturated larger areas of soil and because greater numbers of zoospores were available for infection (10). Populations of *P. parasitica* in tomato field soils at the end of the season were higher in plots furrow-irrigated on a 14-day schedule than in those furrow-irrigated on a 28-day schedule (24) but were not affected by the duration of irri-

gation (21). Populations of *P. cinnamomi* also increased in soil after irrigation of *Eucalyptus marginata* sites in Australia (29,34). Soil water contents were measured in our study at the time of sampling of soil for population densities of *P. capsici* and therefore do not reflect all the fluctuations in soil water content associated with individual irrigation or rainfall events. However, it is probable that repeated periods of soil saturation

with more frequent drip irrigations provided conditions conducive for indirect germination of sporangia and zoospore release in soil (5,9).

Population densities of *P. capsici* also were greater early in epidemic development on the side of the plots where the drip irrigation line was located than on opposite sides of plots in a field with moderate rainfall in Clayton in 1989. In fact, the side of the plot provided a better

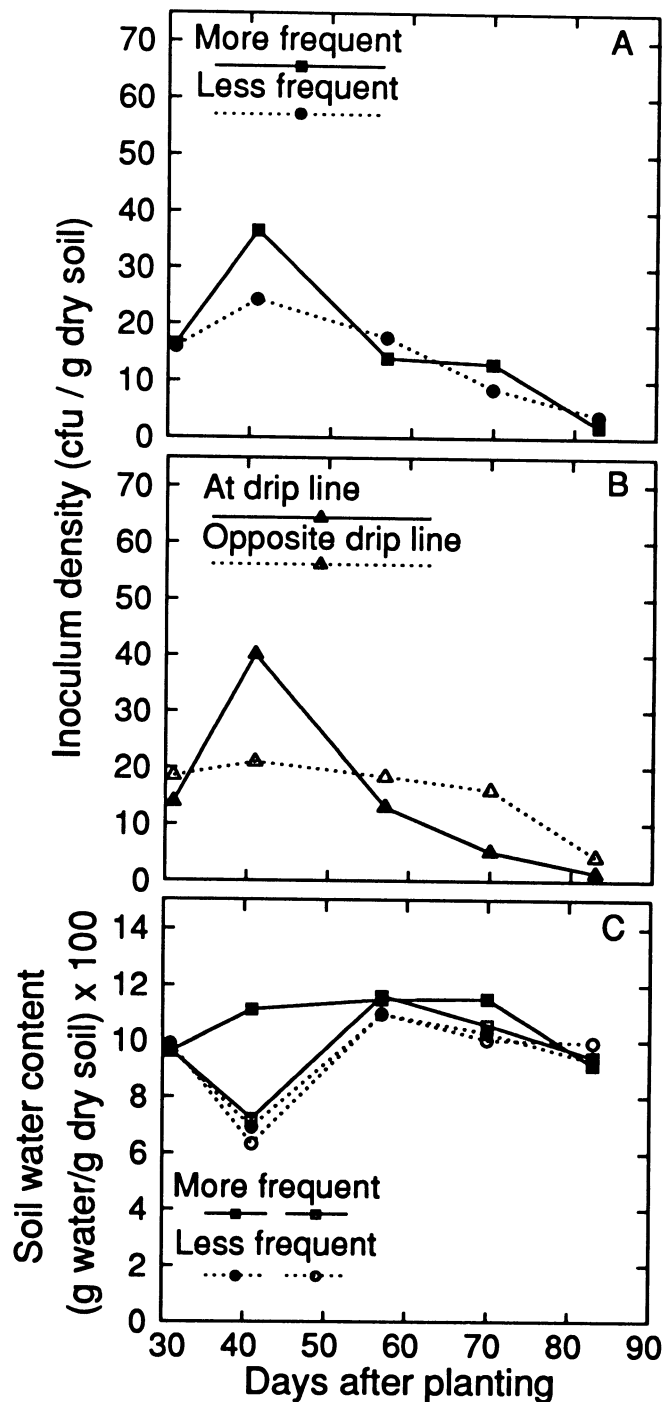


Fig. 3. Population densities of *Phytophthora capsici* in soil and soil water contents at the moderate rainfall field in Clayton in 1989: (A) Population densities over time in soil irrigated on a more frequent or a less frequent schedule. Irrigation main effect means are shown over time. (B) Population densities over time on the side of the plot with the drip irrigation line or on the opposite side. Side main effect means are shown over time. (C) Soil water content at the time of sampling in plots irrigated on a more frequent or less frequent schedule on the side of the drip irrigation line (solid symbols) or on the opposite side (open symbols).

measure of soil water content than irrigation level. Population densities of *P. capsici* in soil may have increased to a greater extent near the drip irrigation line than opposite the drip irrigation line because of more frequent saturation periods and/or increased root production. *P. parasitica* also has been recovered at a higher frequency immediately under drip emitters than away

from the drip emitters in citrus orchards (10). A positive correlation of population densities of *P. parasitica* with feeder root densities has been reported in citrus (10,27). We did not quantify root length densities in our experiments; however, increased root production near drip emitters has been reported in other solanaceous and perennial hosts (3,10, 11). In the field with moderate rainfall,

it is likely that root densities were higher early in the season on the side of the plots where the drip irrigation line was located than on opposite sides of plots irrigated more frequently because soil water contents were higher in this area. Soil water content on the sides of the plots opposite the drip irrigation line in plots irrigated more frequently was similar to soil water content in plots irrigated less frequently. These results have practical implications. Targeting fungicide applications to the sides of plots near drip emitters may improve disease control.

Population densities of *P. capsici* were not significantly affected by irrigation frequency or the location of the drip irrigation line in a field with high rainfall in Clinton in 1988. The magnitude of the fluctuations in population densities also was less in the field with high rainfall than in the field with moderate rainfall. Differences in soil water content between the sides of the plots that were drip-irrigated more frequently were not as large at the high rainfall field than at the moderate rainfall field. Population densities of *P. parasitica* fluctuated less in citrus soils that were drip-irrigated than in those that were furrow-irrigated because changes in ψ_m were less variable under drip than furrow irrigation (18). In our study, even though the fluctuations in propagule densities over time were not as large in the field with high rainfall as in the field with moderate rainfall, population densities at all inoculum levels were sufficient to cause large amounts of disease by the end of the season.

Largest increases in propagule densities in infested plots occurred early after disease onset when the rate of disease was increasing in both fields. Positive correlations between pathogen densities and disease incidence were observed early in epidemic development. Maximum increases in densities of *P. capsici* propagules occurred in soil containing root tissue for colonization by the pathogen. The increases in propagule densities in soil may have been caused by secondary inoculum production and release of zoospores in soil during saturation periods. Propagule densities of *P. p. nicotianae* increased earlier on a susceptible than on a resistant cultivar in the field and declined when disease incidence was high (13,17). Propagules of *P. parasitica* also increased to a greater extent in soil planted to a susceptible citrus rootstock than in soil planted to a resistant one (1), and propagule densities of *P. cinnamomi* were greater in the root zones of azalea plants with mild symptoms than in the root zones of plants with severe symptoms (4). In our work, propagule densities of *P. capsici* decreased dramatically when disease incidence in pepper was high in all infested plots, possibly because severely

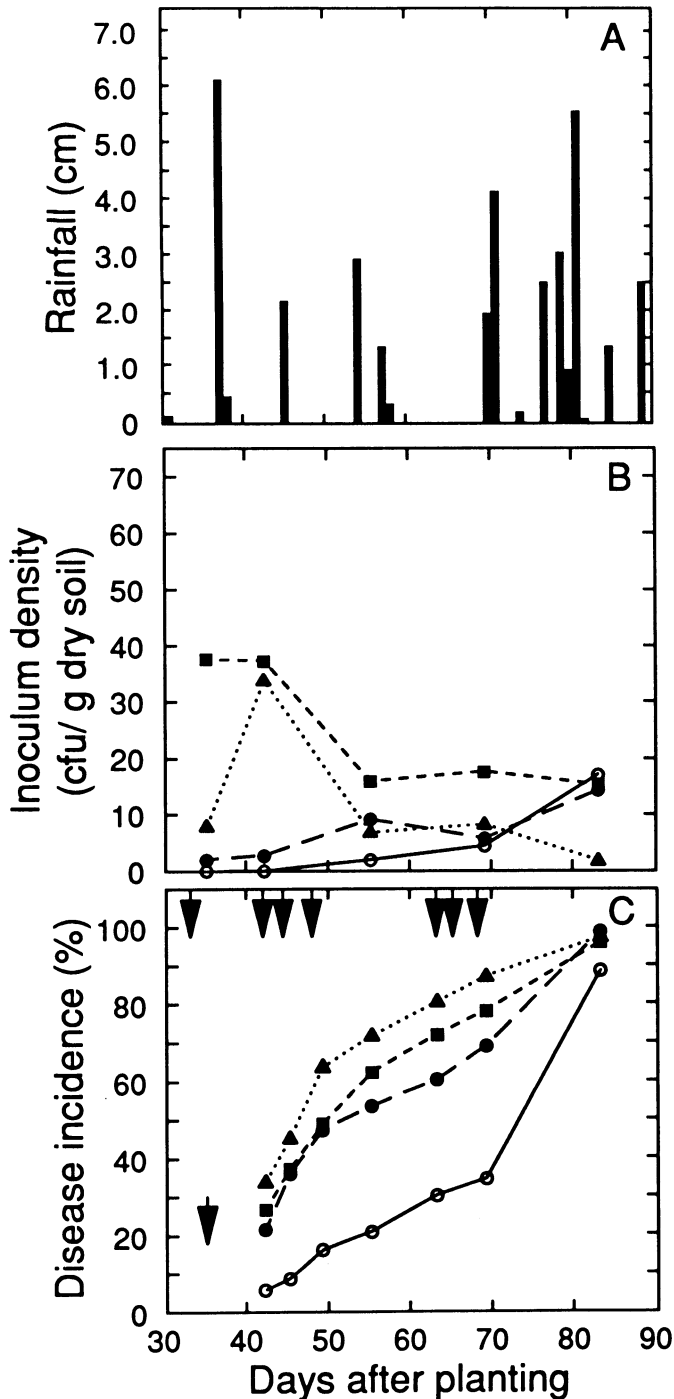


Fig. 4. Total rainfall distribution and progression of *Phytophthora* root rot in bell peppers in plots infested with *P. capsici* at the high rainfall field in Clinton in 1988: (A) Total rainfall distribution. (B) Population densities of *P. capsici* over time in plots uninfested (○) or infested at one of three levels of inoculum (● = 0.01x, ▲ = 0.1x, ■ = 1.0x). Inoculum main effect means are shown over time. (C) Disease incidence over time in plots uninfested (○) or infested at one of three levels of inoculum (● = 0.01x, ▲ = 0.1x, ■ = 1.0x) applied 35 days after transplanting. Disease main effect means are shown over time. Top arrows indicate times of application of drip irrigations, and bottom arrow indicates time of infestation with *P. capsici*.

diseased plants were no longer producing susceptible roots for colonization.

P. capsici was measured in initially uninfested plots after onset of disease at both field locations. Several cycles of secondary inoculum production may have been necessary before propagules were detectable in these plots. Propagules present in soil before symptom expression may have been below the detection threshold of our dilution plate assay. In addition, we measured disease incidence on a more frequent basis than pathogen densities in soil. Population densities of the pathogen in initially uninfested plots at the end of the season were higher in the high rainfall field than in the moderate rainfall field.

Very low levels of inoculum at the time of infestation of the plots were responsible for large amounts of disease in our study. We were not able to determine a threshold population below which negligible disease loss occurred, since even the lowest level of inoculum used resulted in severe disease. The population densities in soil immediately after infestation in most plots except those inoculated at the highest inoculum level were within the range reported to occur in naturally infested fields during disease progress (22).

Plots in this study were artificially infested with mycelium and sporangia of *P. capsici* on a V8 vermiculite medium. In a field with natural inoculum, however, oospores are probably the source of initial inoculum for epidemic development. Production of oospore inoculum for artificial field infestations of the size used in this study would have been impractical. However, our previous work has demonstrated that oospores germinate in the presence of soil or root extracts to form sporangia (15) and zoospore release occurs with periods of soil saturation (16). Thus, zoospores are probably the primary infective propagule responsible for disease in fields with oospore or sporangial inoculum. We did not examine dilution plates to identify the propagule type recovered in this study. However, because only a single mating type was introduced into plots, sporangia, zoospores, and mycelial fragments were the most likely propagule types recovered in the dilution assay. In addition, zoospore germination was high on the medium used in the study. The dynamics of pathogen population changes over time may also differ in soils that are not fumigated and contain a greater diversity of soil microorganisms. Further epidemiological studies need to be conducted in fields with natural inoculum to confirm our results presented here.

More studies are also needed in naturally infested soils to identify the source and density of initial inoculum in grower fields and to identify mechanisms of pathogen dispersal in the field. Although both mating types of the

pathogen have been found in some pepper fields (22,23), more extensive sampling within fields is needed to determine the importance of oospore inoculum in disease development. Because soil water contents can vary widely across a row in drip-irrigated peppers, further studies on root growth responses to irrigation and the effects on subsequent pathogen densities in soil are needed.

Population densities of *P. capsici* in artificially infested field soils were dynamic and were significantly affected by rainfall, frequency of drip irrigation, location of the drip irrigation line, and disease incidence. Management of this disease in the future will require the appropriate timing and location of applications of fungicides to reduce pathogen populations in soil before phases of rapid disease increase. In addition,

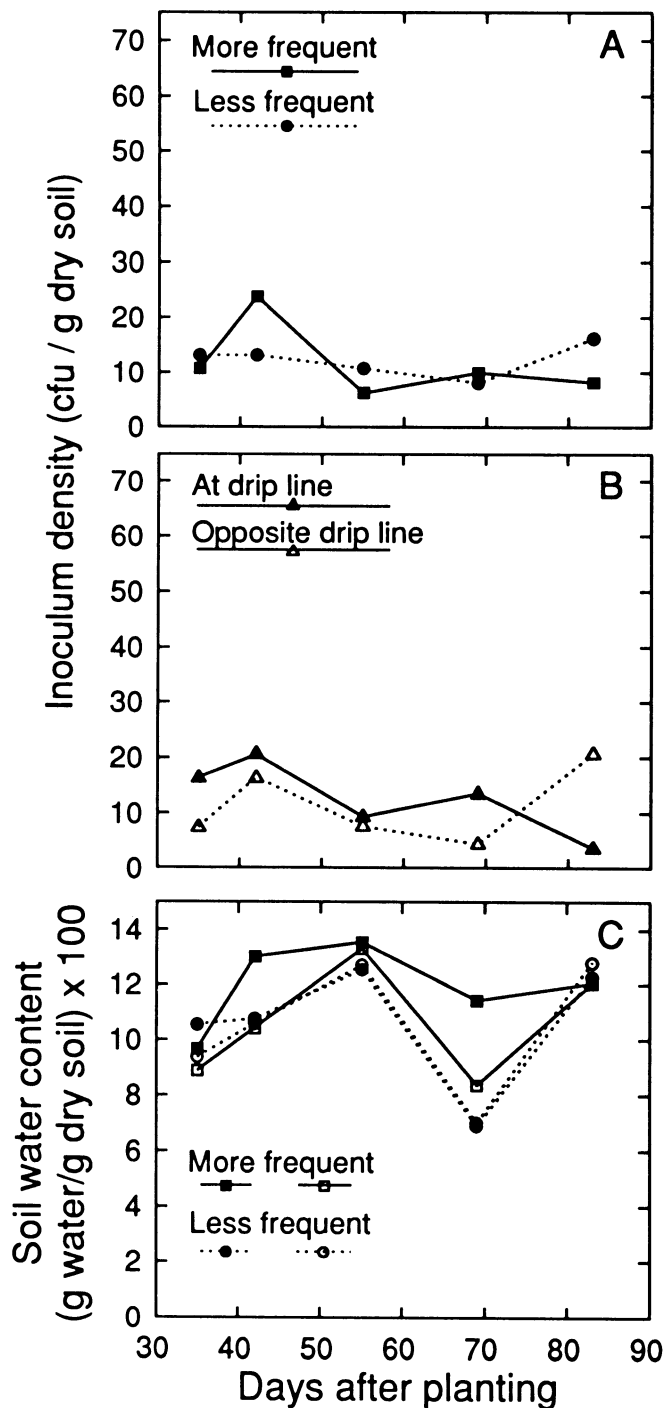


Fig. 5. Population densities of *Phytophthora capsici* in soil and soil water contents at the high rainfall field in Clinton in 1988: (A) Population densities over time in soil irrigated on a more frequent or a less frequent schedule. Irrigation main effect means are shown over time. (B) Population densities over time on the side of the plot with the drip irrigation line or on the opposite side. Side main effect means are shown over time. (C) Soil water content at the time of sampling in plots irrigated on a more frequent or a less frequent schedule on the side of the drip irrigation line (solid symbols) or on the opposite side (open symbols).

cultivars with high levels of resistance may provide an important management strategy in the future, especially in fields with high rainfall where disease can become severe and cannot be managed with changes in irrigation practices.

ACKNOWLEDGMENTS

We thank P. Grand, K. Respass, T. Sullivan, and D. Whittington for technical assistance. The research reported was funded by the North Carolina Agricultural Research Service.

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