

Effects of Furrow Irrigation Schedules and Host Genotype on *Phytophthora* Root Rot of Pepper

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ABSTRACT

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The effect of furrow irrigation regimes on *Phytophthora* root rot of pepper (*Capsicum annuum*) was studied at Davis, California, in the dry summer months of 1990 and 1991. Soil near the roots was artificially infested with inoculum of *Phytophthora capsici* when plants of susceptible cv. Yolo Wonder B were at the seven- or nine-leaf stage, and furrow irrigation was applied every 7, 14, or 21 days. In 1990, disease incidence was higher and onset of above-ground symptoms was earlier with more frequent irrigation. Yield in infested plots irrigated every 21 days did not differ from that in the corresponding noninfested controls, whereas yields in infested soil irrigated every 7 and 14 days were only 45 and 83% of the respective controls. Irrigation schedules in noninfested controls had no effect on yield and had minimal effects on plant water potential. In 1991, while the trend of reduced disease with longer irrigation intervals was conserved, disease level as a whole was higher and no effective root rot control was achieved. The levels of water stress attained in an additional treatment irrigated only once did not enhance disease. Contrary to the results in 1990, more frequent irrigation of noninfested soil in 1991 significantly increased yield and plant water potential. Evidence is presented that the differences in disease development and yield between years were related to temperature effects on plant development. In a separate experiment with genotypes varying in resistance to *P. capsici*, disease increased with irrigation in three genotypes (Yolo Wonder, Adra, and PH28). Three other genotypes (DK1, 2258, and CM328) developed little or no disease, even under extremely moist conditions. While the importance of other environmental factors was illustrated, frequency of irrigation is an important factor in epidemics of *P. capsici* root rot. Effective irrigation management and genetic resistance can reduce disease development significantly.

Phytophthora capsici Leonian was first described in New Mexico (17). Since then it has become recognized as an important pathogen of pepper (*Capsicum annuum* L.) in the United States (1,4,8,30,34) and many other countries (e.g., 15,20,24,25,29). Most common pepper cultivars are extremely susceptible to *Phytophthora* root and crown rot, and chemical control is of limited value under conducive conditions (1,25). Furthermore, isolates of *P. capsici* resistant to fungicides have been selected (2,5). Sources of genetic resistance exist in pepper (11,16,19,27), but incorporation of effective resistance into commercial cultivars has been difficult (24,28) and intermediate levels of resistance may give inadequate control (23,29). On the other

hand, modified furrow irrigation practices were shown to be valuable in reducing *P. capsici* root rot of chile peppers (1). Additional research on the influence of irrigation management on disease development in susceptible and resistant cultivars will help to develop integrated control measures for *P. capsici* root rot of peppers.

The epidemiology of *Phytophthora* root rots is largely dependent on soil moisture and related factors (9). For example, flooding enhanced root rot of peppers (3,13), and root rot and blight of peppers increased with the cumulative amount of rainfall (4). In addition, under low rainfall situations, higher frequencies of drip irrigation resulted in higher levels of the disease (30,33). It was also shown that irrigating alternate furrows, rather than every furrow, can reduce the disease in chile peppers (1). In California, pepper is grown in the dry summer months and mostly furrow irrigated, usually every 7-14 days. Damaging levels of root rot sometimes occur under these conditions. This study attempts to quantify the effects of furrow irrigation schedules on the development of *Phytophthora* root rot of peppers under these conditions. Interactions of irrigation schedules and genotypes with different degrees of resistance to *P. capsici* are also described. A preliminary report has been published (6).

MATERIALS AND METHODS

Experiments were conducted on deep, well-drained Yolo loam soils (pH 7.1, CEC 30 meq/100 g) with no record of *P. capsici* at the Plant Pathology Field Area, University of California, Davis.

Frequency of irrigation experiments.

Pepper cv. Yolo Wonder B was direct-seeded in single rows on 0.75-m-wide beds on 22 May 1990 and 21 May 1991, and thinned to one plant per 25 cm of row. Fifty-two or 48 days after planting, when plants were at the nine (1990) or seven (1991) leaf stage, respectively, the field was divided into four blocks. Experimental units consisted of 12-m-long beds separated by guard rows. Blocks were separated by earthen dams and a 6-m gap to prevent water flow. The experimental design was a randomized complete block with four replicates and six (1990) or eight (1991) treatment combinations (three or four irrigation schedules \times infested and noninfested soil). Inoculum consisted of a mixture of three field isolates grown separately in V8-vermiculite as described (32) and mixed in equal parts on the day of inoculation. Inoculum was rototilled into the furrow wall adjacent to the plants at a rate of 120 ml per linear meter in half of the units, while the remaining units served as uninoculated controls (7). After incorporation of the inoculum into soil, furrows were reshaped so that the inoculum was positioned between the roots and the furrows.

In 1990, differential irrigation schedules, begun after soil infestation, were every 7, 14, and 21 days. In 1991, treatments included the same three schedules and one additional treatment irrigated only once, 35 days after inoculation, when leaf water potential was significantly lower than in other treatments. Water remained in the furrows for 3-5 hr during each irrigation.

Soil and leaf water status were assessed weekly, 24 hr before irrigations were applied. Soil water contents in the center of plant rows were measured at five depths at 30-cm increments up to 150 cm using a neutron probe (7). Probe counts were calibrated by relating count ratios to actual volumetric water contents as described (31). Water-release curves of the soil near the experimental site were determined using tension plates and have been published (7).

Leaf water potentials were measured with a pressure chamber (Model 3005,

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Soil Moisture Equipment Co., Santa Barbara, CA). Measurements were taken on the top fully expanded leaves of two plants in each experimental unit at midday (1990 and 1991) and before dawn (1990 only). Because *P. capsici* root rots cause water stress, and the measurements were designed to monitor the availability of water to plants, evaluations were done only in healthy-appearing plants. Leaf water potentials were compared with Fisher's protected LSD ($P = 0.05$). Air and soil temperatures and evapotranspiration rates were obtained from the California Irrigation Management Information System (CIMIS) network station at Davis.

Genotype vs. irrigation experiment. Another experiment in 1991 examined the response of various *Capsicum* genotypes to *P. capsici* and irrigation schedule. Pepper lines PH28, DK1, CM328, and 2258 (Petoseed Co., Woodland, CA), with different degrees of resistance to *P. capsici*, and cvs. Adra (partially resistant, Abbott and Cobb Seed Co, Feasterville, PA) and Yolo Wonder B (susceptible, Petoseed Co.) were direct-seeded (21 May 1991) or transplanted (18 July 1991) to 0.75-m-wide beds and irrigated uniformly before soil infestation and differentially afterwards. Exper-

imental design was a split-split-plot with two replicates, with planting methods in the main plots, irrigation schedules in the subplots, and genotypes in the sub-subplots. Sub-subplot units were 6-m-long bed segments containing a single row averaging 14 plants. Irrigation furrows ran the full length of the 36-m subplots, and sub-subplots were randomized within subplots to reduce bias due to position effects of the genotypes along rows and furrows. Three beds (two furrows) were left dry between irrigation treatments. All units were inoculated on 26 July with 4,500 ml of *P. capsici* in vermiculite per 36 m of row, and subsequent furrow irrigations were applied every 14 days, every 7 days, or every 7 days with one prolonged (24 hr) irrigation every other week. One additional block was direct-seeded with Yolo Wonder B in noninfested soil and irrigated with the same schedules as the experimental blocks for observation. Soil and plant water status were not measured in this experiment.

Disease and yield assessment. Data on disease incidence were collected weekly by counting the number of wilting plants. At the end of the season, all plants were uprooted to a depth of 30–40 cm and the final incidence and severity of root rot were assessed. The scale used for rating the severity of root symptoms was from 1 to 5, where 0 = healthy, 1 = necrotic rootlets or lesions on secondary roots, 2 = necrotic secondary roots or lesions on primary roots, 3 = lower primary root necrotic, 4 = upper primary

root necrotic, and 5 = collapsed root with no living tissue and lesion frequently reaching crown. Root rot severities for individual plants were averaged for each experimental unit. The pathogen was isolated on selective medium (PARPH) (14,21) whenever root symptoms were unclear and also from nonsymptomatic roots arbitrarily selected. Yield was estimated by measuring the fresh weights of healthy and sunburned fruit. Fruit was harvested from the Yolo Wonder plants 120 days after seeding in the two irrigation experiments and from the commercial cvs. Adra and Yolo Wonder 137 days after seeding (79 days after transplanting) in the experiment with multiple genotypes.

Statistical analyses were performed with the SAS packages (SAS Institute, Cary, NC). The arcsine (square root) transformation was applied to normalize percent data whenever the original data did not conform to the normal distribution. The repeated analysis of variance was used to compare incidence of disease in samples collected consecutively on the same plots (10). Within-group single degree of freedom contrasts were employed when interactions between main factors were significant. When more than two contrasts were included, the $Pr > F$ values were corrected for the Type I error by the Bonferroni procedure (22).

RESULTS

Effects of irrigation schedule on disease development in susceptible cv. Yolo Wonder B. Disease progress and intensity were consistently reduced in treat-

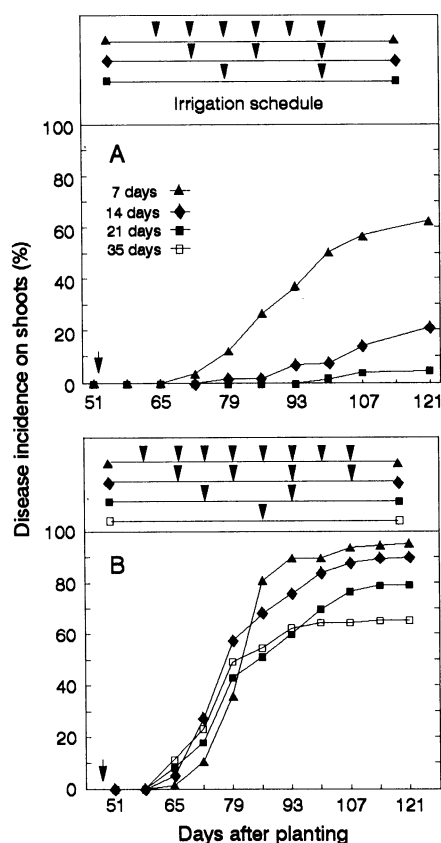


Fig. 1. Progression of *Phytophthora* root rot of pepper (mean of four replicates) in soil infested with *Phytophthora capsici* (A) in 1990 and (B) 1991. Arrow on the x-axis indicates the day when soil was infested, and the arrows on the lines in the boxed area indicate days when differential irrigations were applied.

Table 1. Repeated measures analysis of variance of the incidence of shoot symptoms in pepper plots infested with *Phytophthora capsici* in two growing seasons

Effects	Source	df ^b	Mean square	Wilks' λ	P
Year ^a					
Irrigation effects					
1990	Block	3	0.3747		0.4985
	Irrigation	2	2.8505		0.0290*
	Error	6	0.4213		
1991	Block	3	1,673.56		0.5836
	Irrigation	3	1,525.08		0.6165
	Error	7	2,406.49		
Time*irrigation effects					
1990				0.0195642	0.5951
1991				8.27×10^{-6}	0.0321*

^aPercent data have been transformed to arcsine (square root) in 1990.

^bError degrees of freedom reduced in 1991 due to missing points.

Table 2. Single degree of freedom contrasts for incidence (percentage) of shoot symptoms at harvest in pepper plots infested with *Phytophthora capsici*

Year	Contrast ^a	df	Sum of squares	P ^b
1990	b vs. w	1	3,461.1200	0.0150*
	t vs. w	1	6,838.0665	0.0006**
	b vs. t	1	569.3625	0.9720
1991	b vs. w	1	16.2937	1.0000
	t vs. w	1	338.5551	0.7240
	s vs. w	1	1,341.0150	0.0168*
	s vs. t	1	411.7057	0.5120

^aw = Weekly irrigation, b = biweekly irrigation, t = triweekly irrigation, and s = stressing schedule (1991 only).

^bAfter Bonferroni procedure.

ments irrigated less often, and in 1990 the onset of shoot symptoms was also delayed (Fig. 1A). Almost two-thirds of the plants were wilting or dead at the end of the 1990 season when plots were irrigated every 7 days, while only about 5–20% had symptoms with less frequent irrigations (Fig. 1A). Although disease was severe in all inoculated treatments in 1991, final disease levels were highest with more intense irrigations (Fig. 1B).

The repeated measures analysis of variance for irrigation treatments (between subjects effect) (10) was significant only in 1990 (Table 1), but the significant time*irrigation interaction in 1991

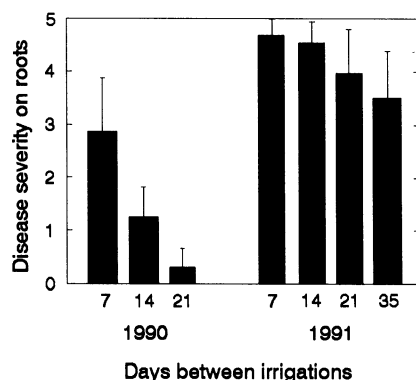


Fig. 2. Final disease severity on roots of pepper plants in soil infested with *Phytophthora capsici* and irrigated every 7, 14, 21, or 35 days in 1990 and 1991, according to the scale: 0 = healthy, 1 = necrotic rootlets or lesions on secondary roots, 2 = necrotic secondary roots or lesions on primary roots, 3 = lower primary root necrotic, 4 = upper primary root necrotic, and 5 = collapsed root with no living tissue and lesion frequently reaching crown. Lines above bars represent the standard deviations of each treatment.

Table 3. Single degree of freedom contrasts for severity of root symptoms at harvest in pepper plots infested with *Phytophthora capsici*

Year	Contrast ^a	df	Sum of squares	P ^b
1990	b vs. w	1	3.5112	0.0684
	t vs. w	1	10.6722	0.0006**
	b vs. t	1	1.9405	0.2946
1991	b vs. w	1	0.0188	1.0000
	t vs. w	1	0.6509	0.6760
	s vs. w	1	2.1600	0.0288*
	s vs. t	1	0.5565	0.8696

^aw = Weekly irrigation, b = biweekly irrigation, t = triweekly irrigation, and s = stressing schedule (1991 only).

^bAfter Bonferroni procedure.

Table 4. Single degree of freedom contrasts within groups (control or infested) for weight of marketable fruits (kg/plot) in pepper plots infested or not infested (control) with *Phytophthora capsici* in 1990

Group	Contrast ^a	df	Sum of squares	P ^b
Control	b vs. w	1	0.2080	1.0000
	t vs. w	1	20.3841	1.0000
	b vs. t	1	16.4738	1.0000
Infested	b vs. w	1	426.4660	0.0654
	t vs. w	1	866.9448	0.0054**
	b vs. t	1	77.3146	1.0000

^aw = Weekly irrigation, b = biweekly irrigation, and t = triweekly irrigation schedule.

^bAfter Bonferroni procedure.

indicated that the rate of disease progress differed among treatments (Table 1). Moreover, the effects of less frequent schedules on reducing the incidence of wilting plants were clear cut and statistically significant in both seasons (Table 2).

In infested soils, more frequent irrigations resulted in greater incidence (not shown) and severity of root rots in both years (Fig. 2, Table 3). *P. capsici* was isolated from roots in all diseased categories (1–5) but was not recovered from category 0 (healthy) roots. No root symptoms occurred in noninfested units.

Fruit yield increased with more spaced irrigations in 1990 in infested soil, while irrigation had no effect on yield in non-infested soil (Fig. 3, Table 4). Yield decreased linearly with increased severity of root symptoms in 1990 ($r = -0.94$). In 1991, despite the fact that yields were uniformly low in infested soil, there was a trend to higher yields with less frequent irrigations (Fig. 3). In addition, in 1991, fruit yield in noninfested soil increased significantly with more intense irrigations (Fig. 3).

The weight of sunburned fruit was significantly affected by the irrigation schedules. Percentages of total fruit weights damaged by sunburn in 1990 varied from 0.2–0.6% in noninfested soil to 2.1, 5.8, and 14.0% in infested units irrigated every 21, 14, and 7 days, respectively. Percent weights of sunburned fruit in 1991 were: 0.7–5.2% in noninfested soil and 11.7, 16.4, 17.4, and 29.6% in infested soil irrigated once at 35 days and every 21, 14, and 7 days, respectively.

Midday leaf water potentials (in non-infested plots) varied between -0.56 and -1.32 MPa and tended to be lower when

soil was irrigated less often than every 7 days. Long-term fluctuations in water potentials (not shown) were a function of weather variables affecting evaporative demands ($r^2 = 0.48$ – 0.54). In 1990, only once was leaf water potential depressed significantly ($P < 0.05$) (by irrigation every 21 days). In 1991, relative to the 7-day schedule, the 21- and 35-day irrigation schedules significantly depressed midday water potentials three and six times, respectively, and the 14-day schedule did so once. The leaf water potentials of apparently healthy plants in infested soil varied in the same fashion, but as disease incidence increased, overall potentials tended to be more negative. In the absence of the fungus there were no effects of irrigation treatment on predawn leaf water potentials, which ranged between -0.11 and -0.21 MPa.

Differences in soil water content among treatments in noninfested plots were usually small (i.e., less than 0.05 at 0.27–0.38 cm³ of H₂O/cm³ of soil). However, at depths of 30 and 60 cm, water contents gradually decreased over the growing seasons and decreased somewhat more rapidly in treatments irrigated less often than every 7 days. On the contrary, there were only slight changes in soil water contents measured at greater soil depths (90 to 150 cm). Moisture levels at 30 and 60 cm were higher in 1991, especially when compared to the water contents of the less frequent irrigation treatments that best controlled disease in 1990. Similar data were collected in infested plots, but as disease

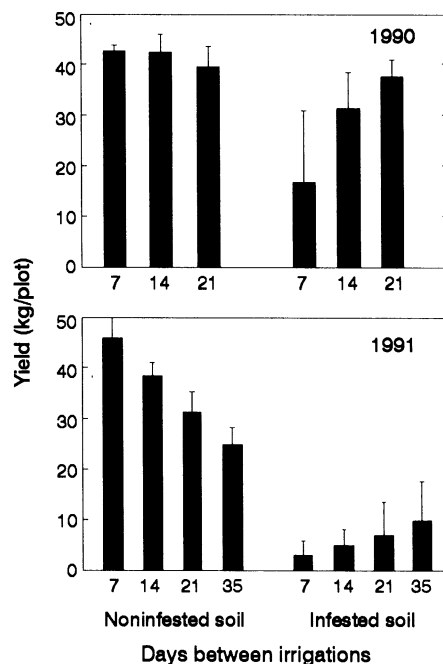


Fig. 3. Fresh weight of pepper fruit harvested from plots not infested or infested with *Phytophthora capsici* and furrow irrigated every 7, 14, 21, or 35 days in 1990 and 1991. Lines above bars represent the standard deviations.

progressed, more water accumulated at all depths.

Average daily air temperatures and ET values before and after soil infestation were very similar in 1990 and 1991 (not shown). Average daily max/min soil temperatures were only slightly lower in 1991 (24.6/22.8 C vs. 23.1/21.5 C before infestation, and 27.2/25.5 C vs. 25.2/23.8 C in 1990 and 1991, respectively, after infestation). While average soil temperatures were similar, the dynamics of soil temperature changes were remarkably different in each year; whereas in 1990, temperatures rose consistently before soil infestation, in 1991 temperatures oscillated widely and were significantly cooler shortly before infestation (Fig. 4).

Genotypes vs. irrigation experiment. Disease progress was also reduced with less frequent irrigations in the genotype vs. irrigation experiment in both transplanted and direct-seeded blocks. In the partially resistant cv. Adra, significant disease developed only when prolonged irrigations were used (Fig. 5). Prolonged irrigation caused severe disease to develop in cv. Yolo, and less intense irrigations reduced disease development significantly (Fig. 5). Root symptoms were also more severe on Yolo than on Adra (not shown). None of the other materials developed significant shoot symptoms, and only line PH28 developed root symptoms with prolonged irrigation. Irrigation ($P = 0.0335$), genotype ($P = 0.0059$), and the interaction irrigation*genotype ($P = 0.0182$) affected final disease levels significantly. Method of planting or the interactions method*genotype and method*irrigation were not significant for any disease variables.

Yields of Yolo Wonder and Adra were significantly reduced ($P = 0.0145$) with heavier irrigations of infested soil, and yield depression due to heavier irriga-

tions was more pronounced in Yolo Wonder than in Adra (not shown). Yields of Yolo Wonder in the noninfested observational plot were 2.6 and 2.2 times the average yields in infested plots irrigated every 7 and 14 days, respectively; yield in noninfested soil was 31 times the average yield obtained in the 7-day extended irrigation regime in infested soil. Although the yields in direct-seeded blocks tended to be larger than the ones in transplanted blocks, planting method was not significant for yield ($P = 0.0613$), and the relationship of smaller yields with heavier irrigations was maintained irrespective of the method of planting.

DISCUSSION

In soil infested with *P. capsici*, more frequent irrigations consistently accelerated the progress of pepper root rot and/or caused higher final disease levels on shoots and roots in three separate field experiments. In all instances, smaller yields were associated with more frequent and heavier irrigations of infested soil.

In 1990, there was no yield reduction when infested units were irrigated every 21 days, while yield was reduced (Fig. 3A) and weight of sunburned fruit increased when infested soil was irrigated more often. Sun damage to fruit was a result of the wilting of leaves due to the root rot. These results are similar to those

of previous studies on *P. capsici* root and fruit rots of squash (*Cucurbita pepo* L. var. *melopepo* (L.) Alef.) (7), and on the effects of alternate furrow and drip irrigation management on *Phytophthora* root rot of peppers (1,30,33). In each case, more moderate levels of irrigation reduced disease and yield loss.

The effects of irrigation on disease development in the 1991 repeat experiment were attenuated by the fact that significant levels of disease developed earlier that year, just about 2 wk after inoculation (Fig. 1B), before the differential irrigations were likely to play an effective part in the disease process. In contrast, in 1990, shoot symptoms developed later, allowing more time for treatments to affect disease development. Nevertheless, final disease levels in both years were affected by irrigation treatments.

Predisposition of crops to *Phytophthora* infections by both excess water and water stress has been demonstrated (e.g., 9,18). However, when significant water stress developed in our experiments, levels of disease were lowest, implying that the levels of water stress attained did not aggravate *P. capsici* root rot of peppers. Conversely, the effects of more frequent or heavy irrigation (Figs. 1 and 5) suggest excess water played an important role. Furthermore, higher disease levels in the 1991 repeat experiment (Fig. 1B) could be due to the higher water contents of the soil at depths of 30 and 60 cm, where most water extraction occurred. In 1990, soil water contents at 30 and 60 cm in the two less often irrigated treatments were usually lower than 0.32 and 0.30 cm³ of H₂O/cm³ of soil, respectively. In 1991, however, soil water contents of all treatments, including the stressed one, were usually higher than 0.32 and 0.30 cm³ of H₂O/cm³ of soil at the same respective depths.

Differences in the physiological development of pepper plants at the time of inoculation may have also contributed to differences in disease development in 1990 and 1991 (Figs. 1 and 2). Although plants were about the same chronological age at inoculation each year, plants were smaller and had only seven leaves in 1991, as opposed to nine leaves in 1990. The most likely condition to have influenced pepper growth in the 2 yr was the fluctuation in soil temperatures before inoculation. In 1991, soil temperatures oscillated widely and almost never were in the optimum range for peppers (24–30 C) (12) for extended periods of time. In contrast, soil temperatures gradually increased with time and were continuously in the optimum range for peppers for most of the period just before inoculation in 1990 (Fig. 4). The effects of age on the reaction of pepper to *P. capsici* infection have been described by several authors (15,19,26,28,29), and *Capsicum* genotypes before the eighth leaf stage

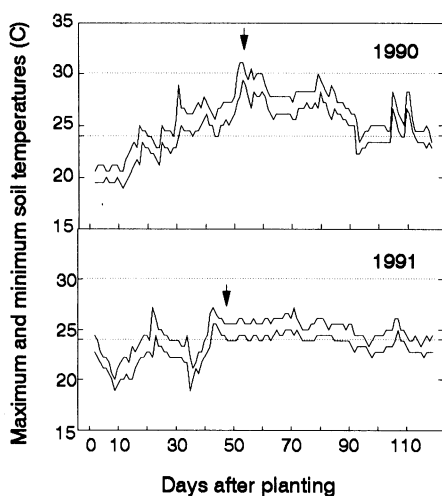


Fig. 4. Daily maximum and minimum soil temperatures recorded at 15 cm depth in the 1990 and 1991 growing seasons. Dotted lines show optimum range of soil temperatures for pepper growth (see text). Arrows indicate the days when soil was infested.

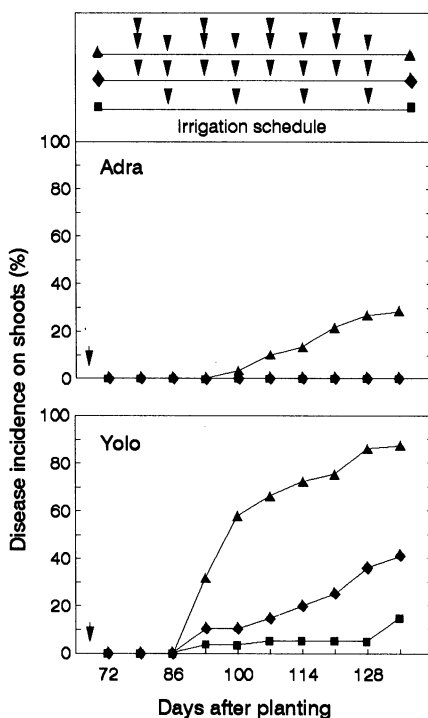


Fig. 5. Progression of *Phytophthora* root rot of pepper in cvs. Adra and Yolo Wonder B (mean of four replicates) in soil infested with *Phytophthora capsici*. Arrow on the x-axis indicates the day when soil was infested, and the arrows on the lines in the boxed area mark the days of irrigations. Duplicated arrows indicate extended irrigations.

(about 7 wk after planting for Yolo Wonder at 25/20 C) are usually cited as extremely susceptible. Overall higher disease levels, earlier disease onset, and larger response to irrigation in noninfested control plots all conform with a slower initial growth of the host. Higher levels of soil moisture that resulted from lower water extraction by slow-developing root systems may also have accelerated disease progression early after inoculation in 1991. All interactions between soil temperature, host susceptibility, and soil moisture may be examined by field experimentation.

In the absence of *P. capsici*, pepper yields were not decreased by less frequent irrigations in 1990 (Fig. 3), as was also the case for Yolo Wonder in the observational plot in the genotype vs. irrigation experiment. These results support a recommendation for longer intervals between furrow irrigations for pepper production. However, in the repeat experiment of 1991, yields in noninfested soil increased in response to more frequent irrigations (Fig. 3). This is an indication that the plants did not have an adequate water supply with less frequent irrigations in 1991, a conclusion corroborated by the significant differences in the plant water potentials that developed often in 1991 but only rarely in 1990. Significant reductions in leaf water potential occurred even when soil moisture levels were higher in 1991 than in 1990, a result consistent with smaller plant sizes, perhaps including smaller root systems, in 1991.

In the genotype vs. irrigation experiment, plants were seeded the same day but inoculated 18 days after the 1991 repeat experiment on just Yolo Wonder, so that plants were physiologically older. With four of the genotypes, more frequent and/or extended irrigations significantly increased root rot incidence, and the least frequent irrigation schedule controlled disease in all materials. Four genotypes that developed disease were ranked DK1 > PH28 > Adra > Yolo for relative levels of resistance to *P. capsici*. Two other genotypes, CM328 and 2258, developed no symptoms, even under extreme disease pressure, suggesting that their resistance is more complete. The prolonged irrigation treatment simulated the situation occurring when very long beds are furrow irrigated in commercial fields. Our results also showed that direct-seeded or transplanted plants were equally susceptible to the root rot.

In general, our results show a strong effect of irrigation management on *Phytophthora* root rot of pepper under a variety of conditions. The results suggest that less frequent irrigations potentially could reduce or control the disease in the field, especially when used in conjunction with relatively resistant cultivars. On the other hand, water stress in the absence of *P. capsici* can decrease

pepper yields, and it will be important to adjust irrigation schedules for variations in available moisture, soil type, plant size, ambient conditions, and other variables, as well as for the risk of *Phytophthora* root rot. Furthermore, the variability of the results between years implies that other factors, especially environmental variables, can have large effects on disease development and pepper yields. However, the epidemiological advantages of reducing the frequency of furrow irrigation were consistently demonstrated.

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