Effects of the Frequency of Furrow Irrigation on Root and Fruit Rots of Squash Caused by *Phytophthora capsici*

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ABSTRACT

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Squash (*Cucurbita pepo* var. *melopepo* cv. Early Summer Crookneck) was grown from seed in field plots initially free of *Phytophthora capsici* at Davis, California. Thirty to forty days after seeding, the soil adjacent to the plants in half of the plots was infested with *P. capsici* propagules. Furrow irrigation was applied uniformly before the soil was infested and every 7, 14, or 21 days thereafter, for both infested and noninfested plots. Disease progress was significantly slower, onset of disease was delayed, and final severity of symptoms on shoots and roots was significantly reduced with decreasing frequency of irrigation. Yields in infested soil irrigated every 14 and 21 days did not differ from the yields obtained in the corresponding noninfested controls. In contrast, the yield in infested soil irrigated every 7 days was only 40% of the yield obtained in the corresponding controls. Yield losses due to the direct infection of fruit were limited to 20% by weight, and the results suggested that root and shoot symptoms had to become severe for yield loss to be significant. In the absence of the pathogen, irrigation frequency had no significant effect on yield or plant water potential, and plants irrigated less often extracted water from deeper soil layers. The results imply that less frequent furrow irrigation is an effective way to reduce losses due to *P. capsici* in squash fields in California.

Phytophthora capsici Leonian can be a destructive pathogen of roots, stems, and fruits of several crop species (22) and is a limiting factor to the production of many cucurbits worldwide. Infections of fruits of cucumber, honeydew melon, cantaloupe, and watermelon by *P. capsici* were first reported in the United States in the late 1930s (17,30,31). In California, Tompkins and Tucker (28,29) were the first to describe root rots of cucurbit species due to *P. capsici*. A more recent survey on the pathogen attacking both pepper and cucurbits was done in North Carolina (23). While most cultivated cucurbit species appear to be susceptible to *P. capsici*, the roots and fruits of all available squash cultivars (*Cucurbita pepo* L. var. *melopepo* (L.) Alef.) appear to be especially susceptible to the pathogen. Furthermore, while fungicides are active against *P. capsici*, they cannot provide adequate control under conducive conditions (e.g., 21).

Diseases caused by species of *Phytophthora* generally increase with the intensity of irrigation, and the importance of saturated soil conditions in promoting infection has been recognized for the genus *Phytophthora* as a whole (9). In the absence of significant rains, irrigation practices have particularly large effects on the development of *Phytophthora* diseases (10). Therefore, there is a need to identify cultural practices, including irrigation, that have potential to reduce the development of root and fruit rots caused by *P. capsici* in squash.

In the Central Valley of California, the summer is very dry and the epidemiology of *P. capsici* diseases can be different from that in other areas, such as Florida (5,9), Maryland (27), and North Carolina (25), where host crops are rain irrigated and the pathogen is splash-dispersed by rain. Under those conditions, *P. capsici* infection of pepper (*Capsicum annuum* L.) increased with the cumulative amount of rainfall (5), in part because of splash dispersal (27). Even under low rainfall, higher frequencies of drip irrigation increased levels of root rot caused by *P. capsici* in pepper (24). Furthermore, limiting furrow irrigation to alternate rows gave adequate control of *P. capsici* root rot of chile pepper under low rainfall conditions (2).

In California, squash is usually furrow irrigated on a schedule empirically found to give high yields. Although practices vary, most producers of squash seed irrigate their crop every 7–14 days. However, when *P. capsici* is present, destructive levels of disease develop on the roots, stems, and fruits of squash grown for seed. The literature contains no quantitative information describing the effects of irrigation practices on *P. capsici* rots of squash in the field. Consequently, the objective of this study was to estimate the effects of furrow irrigation schedules on the development of root and fruit rots of squash caused by *P. capsici* in California. In addition, the effects of irrigation schedule on plant water status and yield were determined. A preliminary report of the results has been published (8).

MATERIALS AND METHODS

Field experiments. Experiments were conducted in the summers of 1989 and 1990 on a deep, well-drained Yolo loam soil (pH 7.1, CEC 30 meq/100 g) originally free of *P. capsici* in the plant pathology field area at the University of California, Davis. On 28 June 1989 and 11 June 1990, squash cv. Early Summer Crookneck was seeded in single rows on 2-m-wide beds. Plant rows were 15 cm from furrows that were irrigated uniformly; final stand after thinning was one plant per 80–85 cm of row. When plants reached the eight- to nine-leaf stage (31 and 41 days after planting in 1990 and 1989, respectively), the field was divided into 24 experimental units, each consisting of one 9-m (1989) or 12-m (1990) segment of row, separated by one guard row on each side. Earthen dams at each end and a 6-m gap without plants separated the blocks. The experimental design for the treatments initiated after division of the field was a randomized complete block with four replicates and six treatment-combinations, i.e., three furrow irrigation schedules with either infested or noninfested soil.

Inoculum and irrigation treatments. At the time the field was divided into experimental units, half of the units were randomly chosen to be infested with a mixture of three isolates of *P. capsici* grown individually in V8 broth–vermiculite (26). Isolates were obtained originally from squash, pepper, and tomato in California, and all were pathogenic to squash in greenhouse tests (A. C. Café-Filho and J. M. Duniway, *unpublished*). At 42 (1989) and 32 (1990) days after seeding, after a brief irrigation, equal volumes of the three isolates were mixed and rototilled into the furrow wall proximal to the plants at a rate of 120 ml per linear meter of row. Irrigation furrows were then established 25 cm from the plants, so that the inoculum remained between the furrow and the plants. Each exper-

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imental unit had its own furrow and water supply, and all units were irrigated briefly and uniformly the day after the soil was infested. Differential irrigation schedules, applied after soil infestation, were every 7, 14, and 21 days, with water standing in the furrows for 4–5 hr in each irrigation. Noninfested controls were treated identically.

Disease and yield assessment. Disease incidence and severity were assessed weekly by rating visual symptoms on the shoots of each individual plant, according to a scale where 0 = healthy shoot, 1 = mild wilt, 2 = severe wilt, 3 = petioles collapsed, and 4 = entire shoot death. Disease severity on roots was evaluated in the 1990 experiment only, 1 day after harvest, when all plants in each experimental plot were uprooted to a depth of 60 cm, washed, and visually rated individually according to a scale where 0 = healthy roots, 1 = lesions on secondary roots, 2 = secondary roots necrotic and/or lesions on primary roots, 3 = lower primary root necrotic, 4 = upper primary root necrotic, and 5 = complete collapse of root system. Individual disease ratings were pooled to assign one overall composite rating for each plot. In order to estimate disease and irrigation effects on seed production, all fruits were harvested when mature at 78 (1989) and 88 (1990) days after planting (in commercial fruit production, crookneck squash is harvested earlier). Healthy and rotted fruit were sorted visually and weighed, and *P. capsici* was reisolated from diseased fruits, stems, and roots on PARPH medium (16,19).

Soil and leaf water status. During the 1990 experiment only, the volumetric soil water content was measured in all experimental units of one of the blocks using a neutron probe (Nuclear Depth Moisture Gauge Model 503, Campbell Pacific Nuclear, Pacheco, CA). Measurements were begun 43 days after planting and were taken weekly on the day preceding each irrigation at 30-cm increments to a depth of 150 cm. The probe readings were calibrated at the end of the season by relating count-ratios to water contents and to bulk densities measured gravimetrically on excavated soil samples (25). Water release curves for each soil depth were obtained with undisturbed cores on tension plates (Fig. 1). Also in the 1990 experiment, predawn and midday leaf water potentials were measured before each irrigation with a pressure chamber (Model 3005, Soil Moisture Equipment Co., Santa Barbara, CA) to describe the water status of plants subjected to each irrigation treatment (effect of disease on plant water status was not the goal of measurements). The top, fully expanded leaves of two healthy-appearing plants were used for water potential measurements in each experimental unit. Because advanced stages of the disease result in water stress irrespective of the availability of water to the plants, only healthy-appearing plants were chosen.

Statistical analyses. Analysis of variance of disease severity was carried out with SAS packages (SAS Institute), including test for normality of data, mean separation, and repeated measures (12) for the data collected consecutively on the same plots. When within-group contrasts were used, the Bonferroni procedure was employed to correct for the Type I error (20).

RESULTS

Effects of irrigation frequency on disease development. In infested soil, the rate and intensity of disease development increased with increasing frequency of irrigation. In the units irrigated every 7 days, about 70% of the plants exhibited shoot symptoms 4 wk after soil infestation (not shown) and practically all plants were dead by the end of both seasons. In contrast, when units were irrigated every 14 or 21 days, disease progress was slower, and the onset of shoot symptoms was delayed (Fig. 2). Using repeated measures analysis of variance, the irrigation schedule affected the severity of shoot symptoms significantly in infested units (Table 1). The time*irrigation effect, testing the rate of disease progress in the different treatments, was also significant for disease severity (Table 1). Severity of disease at the end of both growing seasons was also affected by irrigation schedule ($P < 0.005$) (Fig. 2). There were no disease symptoms in the noninfested plots throughout the duration of the experiments.

Highly significant interactions were found between irrigation and inoculation

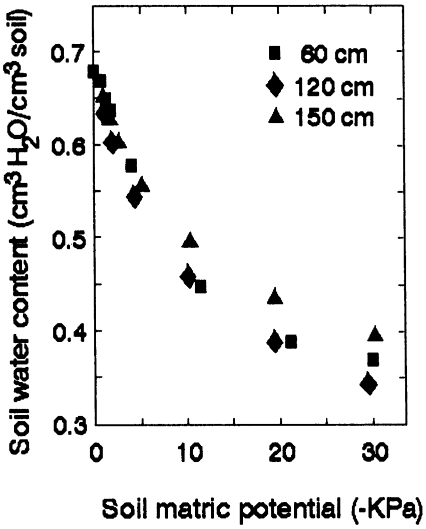

Fig. 1. Water-release curve for samples of Yolo loam soil taken from the experimental plots in 1990. Volumetric water contents were measured from depths of 60, 90, and 120 cm as matric potential was decreased on tension plates.

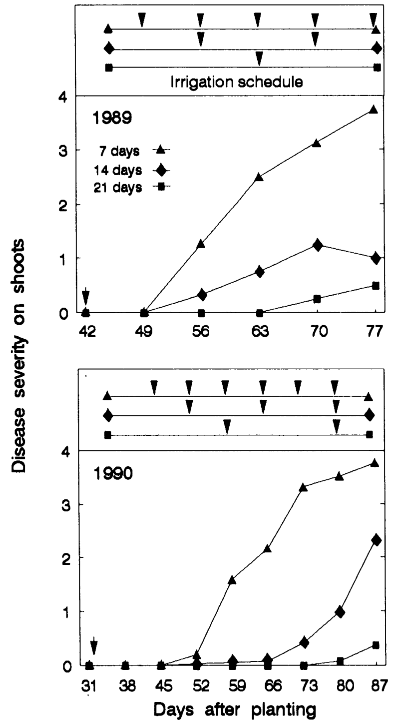

Fig. 2. Progression of Phytophthora root rot on squash in inoculated plots (mean of four replicates) according to irrigation frequencies in 1989 and 1990. The arrow on the x-axis indicates day when soil was inoculated, and the arrows in the boxes indicate the times of differential irrigations.

Table 1. Repeated measures analysis of variance for severity of shoot symptoms in plots of squash infested with *Phytophthora capsici* in 1989 and 1990

Year	Source	df	MS	Wilks' λ	P
Irrigation effects					
1989	Block	3	0.1551		0.9329
	Irrigation[a]	2	26.6875		0.0014
	Error	6	1.1134		
1990	Block	3	0.0898		0.4672
	Irrigation	2	36.2504		0.0001
	Error	6	0.0928		
Time effects					
1989	Time			0.17695	0.0132
	Time*Block			0.13005	0.0630
	Time*Irrig.			0.20804	0.0734
1990	Time			0.03508	0.0854
	Time*Block			0.04675	0.6618
	Time*Irrig.			0.00207	0.0275

[a] 7-, 14-, and 21-day irrigation schedules.

treatments for the final severity of root symptoms ($P = 0.0001$). In infested soil, the final severity of disease on roots was affected strongly by irrigations, and the severity (Fig. 3A) of root symptoms decreased with increasing intervals between irrigations. At the end of the season, incidences of root infection were 100, 79, and 46% with irrigation every 7, 14, and 21 days, respectively. In noninfested controls, there were no irrigation effects on root symptoms, which consisted mostly of small, darkened tissue on finer roots that differed from typical *Phytophthora* lesions in infested units.

P. capsici was consistently isolated from roots with disease severity ratings of 1–5, but not from roots in category 0 (healthy). While *P. capsici* was never recovered from the small, darkened tissue in roots of the plants in the noninfested controls, a *Fusarium* sp. was often isolated.

Effects of irrigation and disease on yield. Significant interactions were found at harvest between irrigation and inoculation treatments on the total yield, and yields of healthy and diseased fruit ($P = 0.0005$–0.0075). In noninfested soil, irrigation had no effect on yield, but in *P. capsici*-infested soil, irrigation affected yield significantly ($P = 0.0006$) and the 7-day schedule reduced yield by 50–60% of that of the controls (Fig. 3B). Furthermore, the yield of healthy fruit from each unit was correlated negatively with the final mean severity of root symptoms ($r = -0.66$). While the proportion of fruit with lesions or rot caused by *P. capsici* was always below 20% by weight, significantly more fruits were diseased in the units irrigated every 7 days in infested soil than in the units irrigated less often (single degree of freedom contrasts highly significant). *P. capsici* was isolated consistently from diseased fruits.

Soil and leaf water status. At the time of soil infestation, soil water contents were uniform among treatments at all depths. Subsequently, while water contents remained high at the shallower depths (i.e., 30–60 cm, data not shown), the soil became progressively drier with less frequent irrigations at greater depths (90–150 cm, e.g., Fig. 4). Data for the infested plots followed a similar trend, but when disease levels were high, more water accumulated in all layers.

Despite the differences in soil moistures, there were no significant effects ($P \leq 0.05$) of irrigation schedules on leaf water potentials measured midday or predawn in noninfested plots (Fig. 5, only midday potentials shown). Correlation analysis (not shown) indicated that midday water potentials were influenced by ambient conditions affecting evaporative demands, and not with irrigation variables. Leaf water potentials of healthy-appearing plants in infested units followed the same trends shown in Figure 5.

DISCUSSION

Results of 2 yr of experiments simulating field practices commonly used by squash seed growers showed that in the presence of *P. capsici,* less frequent furrow irrigation reduced disease progress, delayed the onset of shoot symptoms, and reduced final symptoms on shoots and roots. With the most frequent 7-day irrigation often used by growers, total yield was reduced 50% relative to noninfested controls (yield of healthy fruit was 40% of noninfested controls). In addition, yields in infested soil irrigated every 14 or 21 days were not reduced when compared to noninfested controls. Similar results have been observed in separate studies with pepper (6).

In noninfested control plots, there were no irrigation effects on midday or predawn leaf water potentials or on yields, showing that less frequent irrigations, adequate for disease control, were also appropriate for plant growth. Nevertheless, healthy squash plants wilted frequently at midday, even when the soil was moist and the water potentials of the leaves were −0.7 to −0.9 MPa, suggesting lack of osmotic adjustment (rather than lack of water). Other crops, like pepper, do not wilt at even lower potentials (−1.0 to −1.2 MPa) (6), and the visible wilting may cause squash growers to irrigate frequently. The progressive decrease in soil water contents at depths ≥90 cm when the crop was less irrigated is evidence of increased water extraction, which may have accounted for the lack of stress in leaves. Measurements of soil water content in the infested plots paralleled those shown in Figure 4, indicating that water supply was also adequate in *P. capsici*-infested soil, especially considering that water consumption of diseased plants is reduced. Therefore, on soils with sufficient moisture levels and profiles allowing

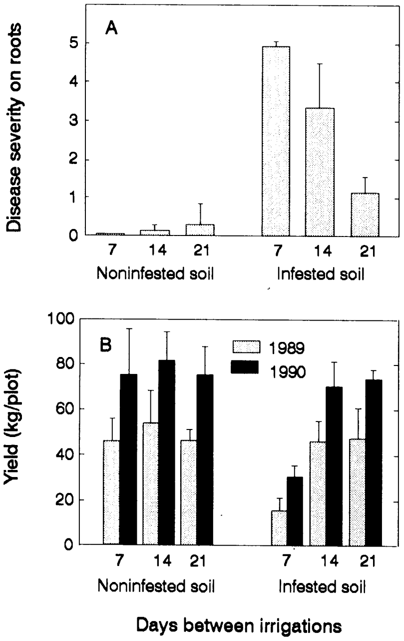

Fig. 3. (A) Mean final disease severity on roots in the 1990 experiment and **(B)** total yield of fruit in 1989 and 1990 in soil not infested or infested with *Phytophthora capsici.* Lines above bars represent standard deviations.

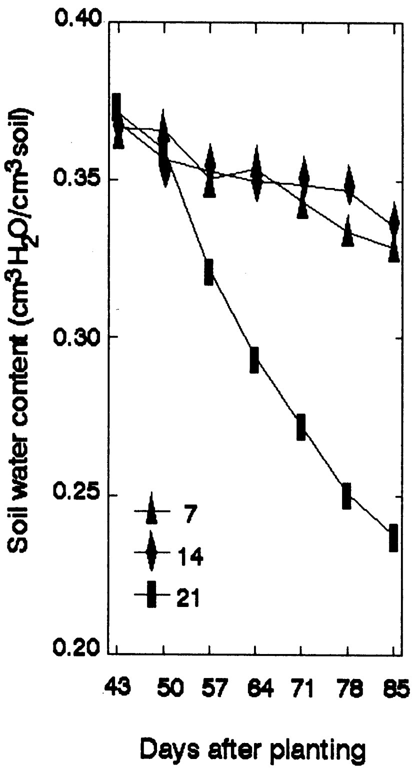

Fig. 4. Volumetric water contents of the soil from noninfested plots in the 1990 season at a depth of 120 cm. Irrigation treatments were every 7, 14, and 21 days.

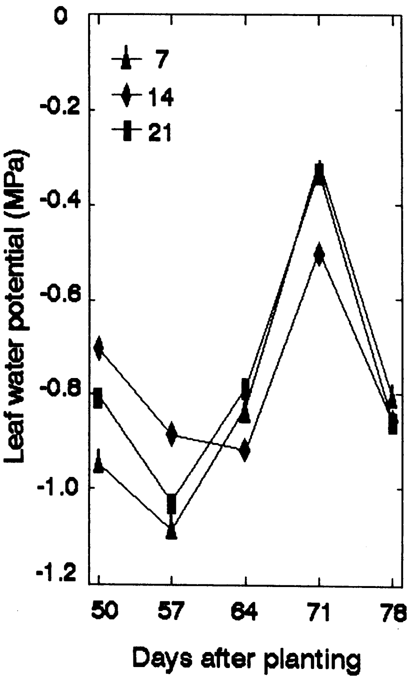

Fig. 5. Midday leaf water potentials in noninfested plots in the 1990 season. Irrigation treatments were every 7, 14, and 21 days.

adequate rooting, less frequent irrigations reduce disease progress and increase seed production. Fewer irrigations are likely to be appropriate for fresh fruit production as well.

In spite of differences in inoculation methods, population density, and distribution of inoculum, several studies showed increased irrigation and soil moisture to increase Phytophthora rots in several hosts (e.g., 11,26,33). Periodic flooding augmented mortality of pepper in soil infested with *P. capsici* oospores (3,13), and *P. capsici* root rot of chile pepper was reduced by limiting irrigation to alternate furrows (2). In addition, Ristaino (24) found *P. capsici* root and crown rot of pepper to be independent of inoculum densities but dependent on frequencies of drip irrigations or rains.

While soil moisture is important, *P. capsici* infection under rain or sprinkler irrigation is expected to be higher because of splash dispersal. Several authors (4,18,27,32) described the aerial phase of *P. capsici* blight of pepper under rainy conditions and discussed the importance of rainfall and splashing of rain drops (5,27). Because it has caducous sporangia (15,23), *P. capsici* is well adapted to splash dispersal, but the lack of rains and the irrigation method chosen here precluded the onset of an aerial phase in our experiments.

The rapid progress of Phytophthora root rot of squash in our experiments is certainly related to the use of a very susceptible host in close proximity to inoculum that was uniformly distributed. Nevertheless, frequent furrow irrigations increased disease development because, 1) soil moisture remained high between irrigations, and 2) there was an increase in the number of events when the soil was flooded with water. A volumetric water content higher than 0.3 cm^3 of H_2O/cm^3 of soil was maintained throughout the season for the two most irrigated treatments, but not for the least (21-day) irrigated treatment (Fig. 4). At this water content, soil matric potential is approximately −30 KPa in the experimental site (Fig. 1), which is favorable to sporangial formation and indirect germination (1). The frequency with which soil is saturated by irrigation is also important because sporangia already produced in the infected roots will release zoospores when wetted (14). Each time furrows were flooded, water probably induced zoospore release and helped zoospore dispersal to the roots as well. Furthermore, saturated or near-saturated conditions caused by irrigations may have also promoted the formation of additional sporangia. While our experiments used uniformly distributed inoculum, more complex interactions of irrigation management and inoculum distribution probably occur in commercial fields. We observed that *P. capsici* survived in the soil of our experiments in the absence of the host and caused high levels of disease the following season (7).

While root lesions were observed in all inoculated treatments, yield reductions were observed only in the treatment with severe shoot symptoms (Fig. 3B). Squash did not show even mild shoot symptoms until a large part, or the uppermost part, of the root system was affected, when plants rapidly collapsed. For example, the significant amount of root rot found at harvest in the treatment irrigated every 14 days (Fig. 3A) was not reflected in a high level of shoot symptoms until fairly late in the season (Fig. 2B) and caused little yield reduction (Fig. 3B). This suggests that an undetermined threshold level of root damage for yield loss was not attained until relatively late in the season, when the fruits were already formed. The majority of yield reduction was due to attack on the roots occurring early enough in the crop cycle to affect production.

In conclusion, it appears that less frequent furrow irrigations, while providing adequate moisture for squash plants to produce high yields, are effective in reducing disease and yield losses caused by *P. capsici*. Further improvements in reliability of these conclusions can be achieved by conducting experiments at locations with different soil types and evaporative demands that may modify the results reported here. For example, sandier, shallower soils and hotter, drier climates could induce plant stress in the less irrigated treatments. Still, the results suggest that *P. capsici* root rot of squash can be managed better in the Central Valley of California by extending the intervals between irrigations, helping to optimize the use of water resources without compromising commercial yields.

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