

## Effects of Irrigation on Buckeye Rot of Tomato Fruit Caused by *Phytophthora parasitica*

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### ABSTRACT

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The influence of irrigation frequency on the incidence of buckeye rot of green tomato fruit was studied in a field plot infested with *Phytophthora parasitica*. The incidence of fruit infections during the final days before harvest in 1980 was significantly higher after a 4-day interval between irrigations than after a 25-day interval between irrigations. In 1982, irrigations were applied every 4, 8, 16, or 32 days throughout the last 64 days of crop growth. The rate and incidence of infection of fruit sampled during the final irrigation increased significantly as the interval between prior irrigations was decreased. Furthermore, the final incidence of infection on fruit grown in the field increased from 24 to 84% as irrigation frequency

increased from once every 32 to once every 4 days. Yield of healthy fruit declined as irrigation frequency increased from every 16 to every 4 days. When soil samples collected 3 days after an irrigation were flooded in the laboratory, 80% of cherry tomatoes floated over the samples were infected by *P. parasitica* within 6 hr. In contrast, infection was less than 10% for fruit floated for 16 hr over soil collected from furrows that had not been irrigated for 28 days. The results suggest that the inoculum of *P. parasitica*, probably in the form of zoospores, is formed more rapidly and abundantly when previous irrigations have been frequent and have not allowed the soil to dry extensively.

### MATERIALS AND METHODS

Buckeye rot of green tomato (*Lycopersicon esculentum* Mill.) fruit has been reported to be caused by *Phytophthora parasitica* Dastur (3,21), *P. capsici* Leonian (3,21), and less frequently, by *P. cryptogea* Pethyb. and Laff. (24), *P. drechsleri* Tucker (3,24), and *P. mexicana* Hotson and Hartge (11). Lesions that develop on the surface of infected fruit have a characteristic pattern of alternating light- and dark-brown concentric rings (14,22,24) resembling a buckeye (14,22). Mycelial growth on the fruit surface, which occurs only under conditions of high humidity (24), has been observed in storage, but is rarely found in the field (22). In contrast to tomato fruit infected by *Pythium* spp., which become soft and watery (19), fruit with buckeye rot remain firm as decay progresses (22,24).

Several investigators have reported that buckeye rot occurs primarily on fruit lying on or near moist soil (14,20,22,24,29). Large amounts of rainfall within a short period of time (14,29) or a single heavy irrigation (24) may result in the sudden appearance of buckeye rot. Rosenbaum (20) demonstrated that a high incidence of buckeye rot occurred only when tomato fruit were placed in soil that was saturated either by watering in pots or by irrigation in the field. Flooded or saturated soil conditions stimulate *P. parasitica* to release zoospores (2,23), and zoospores of *P. parasitica* have been detected within 10 min when soils collected from citrus orchards were flooded (23). Whether such a rapid release of zoospores occurs after the onset of irrigation in tomato fields is not known, and the net effects of the frequency and duration of irrigation on the development of buckeye rot in the field have not been studied.

Fresh market tomatoes grown in California's San Joaquin Valley, where there is little rainfall during crop growth, are usually furrow-irrigated. Buckeye rot, which in this area is most often caused by *P. parasitica*, causes large reductions in the yield of harvestable fruit in fields where many fruit lie on or hang close to furrows during and after irrigations. Yield reductions are greatest during the fall season when growers may irrigate frequently to delay ripening and increase the weight of the fruit. Frequent or heavy irrigation is known to increase the severity of other diseases caused by soilborne *Phytophthora* spp. (28,30,31). In this paper, we report on some effects of irrigation on the incidence of buckeye rot of green tomato fruit caused by *P. parasitica*. A preliminary report has been published (13).

**Field studies.** The experiments reported here were conducted in 1980, 1981, and 1982 in an 841-m<sup>2</sup> field plot located at the University of California, Davis. Soil in the plot is a moderately coarse-textured Yolo loam and at the surface it contains 20–25% clay, 30–40% sand, and 40–45% silt. Undisturbed cores of soil (7.6 cm high, 7.6 cm diameter), obtained from the surface at eight sites in the plot 2 wk after cultivation and 5 days after irrigation, had an average bulk density of 1.4 g/cm<sup>3</sup>. Soil in the plot was infested with *P. parasitica* by burying one infected tomato fruit per meter in each furrow of the plot in 1977 and 1978. In subsequent years, the fungus was repeatedly isolated from green tomato fruit in the plot and was identified as *P. parasitica* from descriptions in the literature (21,22,26,27). The field appeared to be uniformly infested with *P. parasitica* because tomatoes with characteristic buckeye symptoms occurred throughout the plot in preliminary assays in 1979 and 1980.

Tomato seedlings of the fresh market cultivar Cal Ace were started in the greenhouse each year and transplanted into the plot in early May. Rows of plants were centered on raised beds 0.6 m wide with furrows ~15 cm deep between the beds. Immediately after planting, 2.5 cm of water (total land area basis) were applied in all plot furrows, but subsequently the frequency and duration of irrigations were varied as described below. The plot received preplant and sidedress fertilizations totalling 95 kg/ha N and 45 kg/ha P, but no other chemicals were applied. Soil temperature was measured 4–8 cm beneath the soil surface of the side of the furrow using a recording thermograph.

Buckeye rot was often observed in the fall in fields where two or more irrigations occurred within a period of several days. Therefore, the 1980 field plot was established to determine the influence of the length of the interval between irrigations on the incidence of disease. Mature plants were established during a 90-day period in which all furrows were irrigated every 10 days, providing a total of 63 cm of water. The plot was then divided into four blocks in a randomized complete block design. Test furrows within blocks were 14 m long and were each separated by two furrows that were not subsequently irrigated. For the experiment, the final irrigation was preceded by either a 4- or 25-day interval without irrigation. This was accomplished by withholding irrigation from all furrows for 21 days; then half of the test furrows received a 4-hr (5-cm) irrigation. Four days later, all test furrows were given a final 16-hr (10-cm) irrigation. To determine the effect

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of the irrigation interval on the incidence of disease, green tomato fruit (cultivar Castlemart) were placed in the furrows and were sampled throughout the 16-hr irrigation. At the start of the irrigation the fruit (150/furrow) were evenly spaced, blossom end down, along each furrow and were gently pressed into the mud. Beginning 2 hr after the onset of irrigation, and hourly thereafter through 16 hr, 10 fruit were randomly sampled from each test furrow. Fruit sampled 4 hr after the onset of irrigation, and thereafter, were dipped in 400  $\mu\text{g}/\text{ml}$  sodium hypochlorite, rinsed in water, air-dried, and placed in individual plastic bags. Fruit sampled 2 and 3 hr after irrigation began were treated identically except that the sodium hypochlorite wash was omitted to prevent possible eradication of early infections. Controls consisted of tomatoes not placed in contact with soil or irrigation water. All fruit were incubated at room temperature for 7 days. Most infected fruit were identified by the alternating light and dark concentric rings that characterize buckeye rot. Fruit with ambiguous symptoms were considered infected if *P. parasitica* was isolated from them on a modified PVP medium (17).

The effect of long-term variation in irrigation frequency on the incidence of buckeye rot was studied in 1982. The plot was planted and divided into blocks as previously described. Immediately after planting, furrows were irrigated with 6 cm of water. For a period of 64 days, beginning 2 wk after planting, test furrows on either side of each plant row were irrigated together to provide 5 cm of water every 4, 8, 16, or 32 days. Soil matric potential ( $\psi_m$ ) was measured with tensiometers placed at the center of test furrows to a depth of 8 cm beneath the soil surface. The 64-day period ended with a 14-hr, 9-cm irrigation of all test furrows. Infection was evaluated during the final irrigation by placing green tomato fruit (cultivar Castlemart) in the furrows, sampling them at intervals during the irrigation, and observing symptoms as in 1980. Immediately before the final irrigation, 1-L soil samples were collected 2–3 cm beneath the surface of three sites at 4-m intervals in each test furrow. Samples from the three sites were bulked in a plastic bag, sealed and stored at 13 C. Water potential of the samples ( $\Psi$ ) was determined by using a thermocouple psychrometer (5).

In order to determine the effect of irrigation frequency on the incidence of disease at the time of harvest, which occurred 13 days after the final 14-hr irrigation in 1982, infected green fruit that had grown on the vines and were lying on or hanging within 2.5 cm of the soil were counted. Additionally, healthy fruit from each plant were harvested and weighed. Yield (metric tons per hectare) was then estimated from yields recorded as kilograms per plant, after calculating that the average 27 plants per 14  $\times$  0.6-m plant row would represent  $\sim$ 13,000 plants per hectare.

**Zoospore release from soils.** In the laboratory, green cherry tomatoes were used as bait (8,23) to detect zoospores of *P. parasitica* released into surface water after soil samples collected from the 1980 field plot were flooded. Soils with moisture conditions similar to those at the time of the final 16-hr irrigation in the 1980 field experiment were obtained by collecting samples 3 or 28 days after an irrigation. Samples were collected 2–3 cm beneath the soil surface in the manner described for the 1982 field plot. After removing large soil clods and thoroughly mixing the soil from each furrow to ensure a composite sample, a 1-L subsample was evenly dispersed within a plastic container (31 cm long  $\times$  23.5 cm wide  $\times$  10 cm deep). Wire racks were placed over the soil surface to prevent direct fruit contact with the soil. The soil was flooded with 2 L of distilled water and the green fruit (cultivar 026 cherry) were added immediately thereafter. Control fruit were floated in water without soil. At intervals, five fruit were removed from each container and incubated in a moist chamber at room temperature. Numbers of fruit infected with *P. parasitica* were determined after 7 days. Excess soil not used in the experiment was saved for determinations of water content and  $\Psi$ .

The hypothesis that zoospores were the propagules of *P. parasitica* that infected tomatoes in flooded soils was tested by repeating the baiting experiment using 10- $\mu\text{m}$  nylon mesh (Tetco, Inc., 420 Sawmill River Road, Elmsford, NY 10523) to enclose soils before flooding. Motile zoospores confined beneath the mesh in a microbeaker were observed to swim through the 10- $\mu\text{m}$  openings in

the mesh, but the openings were too small to permit passage of sporangia, chlamydozoospores, or oospores. Soils from the 1982 field plot were sampled immediately before the final irrigation and the experiment was done by the methods described above except that the soils were enclosed in the mesh before flooding.

## RESULTS

**Field studies.** The application of two irrigations within a 4-day period in August 1980 resulted in infections of many fruit introduced immediately prior to the second irrigation. Two hours after the second irrigation began, 7.5% of tomatoes lying in furrows which had been irrigated 4 days earlier were infected by *P. parasitica*, and the incidence of infection reached 91% at 16 hr after the onset of irrigation (Fig. 1). In contrast, in furrows irrigated for the first time in 25 days, there were no infections until 7 hr after the onset of irrigation and the incidence of disease never exceeded 25% (Fig. 1). The differences in infection in furrows receiving 4- or 25-day intervals between irrigations were significant ( $P = 0.05$ ) at every sampling interval beginning 3 hr after the onset of the second irrigation (Fig. 1). None of the control fruit were infected by *P. parasitica*.

Long-term variations in irrigation frequency (irrigations applied every 4, 8, 16, or 32 days during a 64-day period in 1982) resulted in significant differences in infection of tomato fruit by *P. parasitica* during a final 14-hr irrigation. Fig. 2 shows that the rate and final incidence of infection of introduced fruit increased as the interval between irrigations decreased. Three hours after the onset of the final irrigation, and at every sampling interval thereafter (except 9 hr), significantly ( $P = 0.05$ ) greater infection occurred in furrows previously irrigated every 4 days than in furrows irrigated every 8, 16, or 32 days (Fig. 2). The differences between results for furrows previously irrigated every 8 days and those irrigated every 16 or 32 days were also usually significant beginning 4 hr after the onset of irrigation. Differences between fruit infection in furrows irrigated

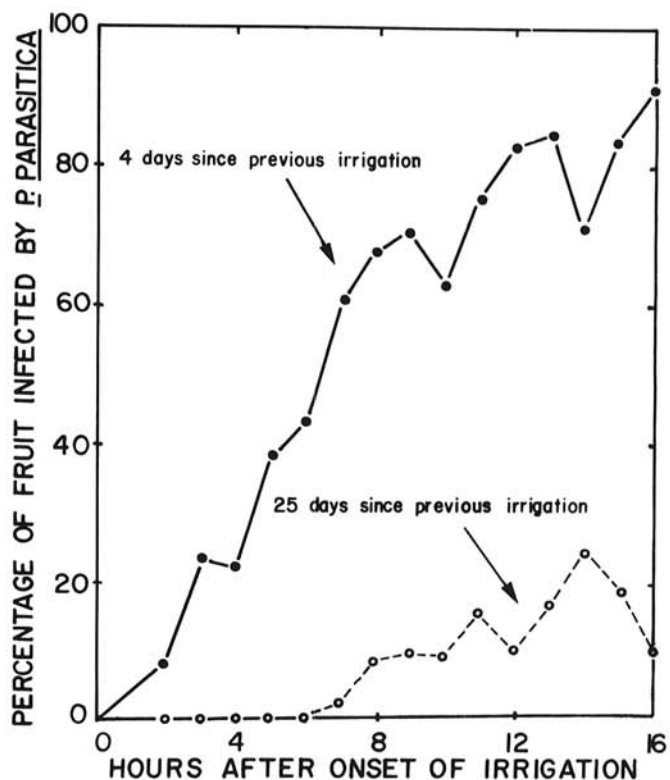


Fig. 1. Incidence of buckeye rot caused by *Phytophthora parasitica* in green tomato fruit sampled at hourly intervals after the onset of an irrigation following either a 4-day or a 25-day period without irrigation. Percentages represented by each data point were calculated by averaging the number of fruit infected by *P. parasitica* in eight replications of 10 fruit each. LSD = 15.3 at  $P = 0.05$ .

every 16 and every 32 days were generally not significant (Fig. 2). None of the control fruit were infected by *P. parasitica*. Tensiometer measurements showed that the  $\psi_m$  of soil 8 cm beneath the furrow surface gradually declined from 0 to between -200 and -400 millibars (mb) during 4-day intervals between irrigations and to between -600 and -800 mb during 8-day intervals between irrigations. When intervals between irrigations were longer than 8 days,  $\psi_m$  dropped below the lowest level ( $\sim$ -800 mb) that can be effectively measured by the tensiometers. The  $\Psi$  of soil samples collected 2-3 cm beneath the furrow surfaces immediately before the final irrigation averaged -4.0, -7.6, -26.2, and -62.6 bars for furrows that had been irrigated every 4, 8, 16, or 32 days, respectively.

Thirteen days after the final irrigation, disease incidence on low-hanging fruit grown in the plot was 24% in furrows previously irrigated every 32 days, and increased to 48, 60, or 84% in furrows previously irrigated once every 16, 8, or 4 days, respectively (Fig. 3A). Furthermore, regression analysis demonstrated a highly significant ( $P = 0.01$ ) and positive correlation between the number of irrigations and final disease incidence (Fig. 3A). A decrease in irrigation frequency from once every 4 days to once every 8 days resulted in reduced incidence of disease (Fig. 3A) and an increase in yield from 19.4 ( $\pm$ 2.3) to 29.0 ( $\pm$ 2.4) metric tons per hectare (Fig. 3B). Another slight increase in yield, from 29.0 to 31.7 ( $\pm$ 4.6) metric tons per hectare, resulted when irrigation frequency was further reduced to once every 16 days. Although disease was slight in furrows irrigated every 32 days (Fig. 3A), poor plant growth resulted in a yield of only 18.4 ( $\pm$ 2.3) metric tons per hectare (Fig. 3B). Results like those in Fig. 3A were obtained in a similar

experiment in 1981, when 79% of the fruit were diseased on plants irrigated every 6 days, and infection decreased significantly ( $P = 0.01$ ) to 68 and 49% when plants were irrigated every 8-10 days and every 15-18 days, respectively. During the months of May, June, and July, temperatures 4-8 cm beneath the soil surface averaged 24 C in 1981 and 23 C in 1982. Daily maximum and minimum temperatures for both years ranged between 22 and 35 C and 12 and 23 C, respectively. These soil temperatures are within the range favorable to growth and infection by *P. parasitica* (9,18).

**Zoospore release from soils.** Cherry tomato baits became infected by *P. parasitica* when sampled within 15 min after flooding soil collected from furrows irrigated 3 days previously (Fig. 4). Infection increased rapidly during the first 5 hr after flooding soil from furrows irrigated 3 days previously, and 100% infection occurred at 16 hr. There were no infections until 2 hr after flooding soil that had not been irrigated for 28 days, and the incidence of disease never exceeded 10% (Fig. 4). According to *t*-tests, the differences in infection for fruit floated over soils irrigated 3 days or 28 days previously were significant ( $P = 0.05$ ) at every sampling interval starting 90 min after flooding. There were no infections of control fruit which were floated in water without soil. Before flooding, soils collected from furrows that had been irrigated 3 and 28 days previously averaged -1.9 and -219 bars  $\Psi$ , respectively.

It appears that zoospores were responsible for infections because many of the cherry tomatoes placed in water over soils contained within 10- $\mu$ m mesh became infected by *P. parasitica*. The rate of infection varied with soil  $\Psi$  and the frequency of prior irrigation in the field. Some fruit became infected when sampled within 25 min after flooding soil from furrows previously irrigated every 4 or 8

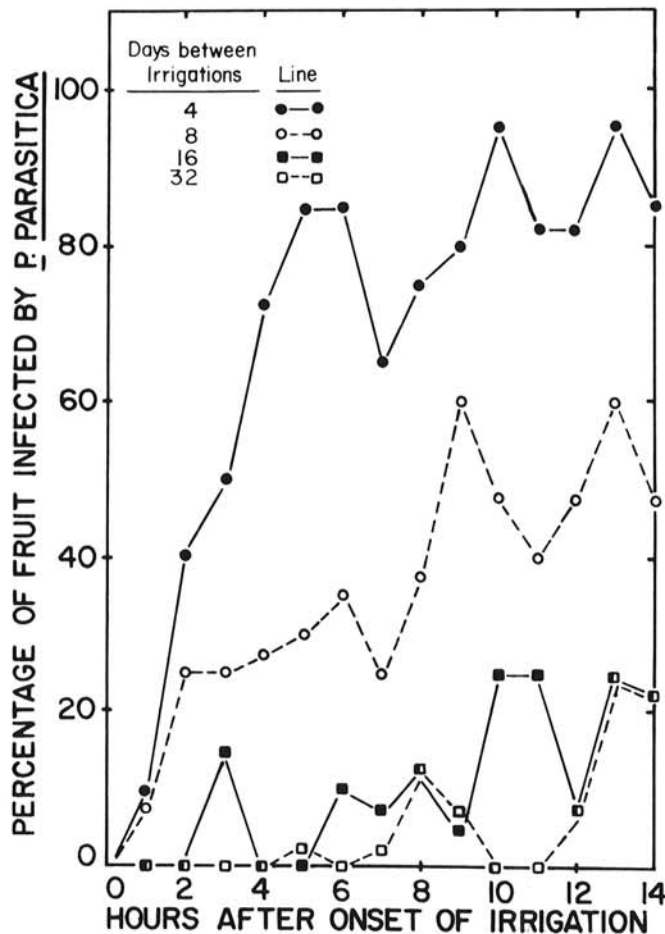


Fig. 2. Incidence of buckeye rot caused by *Phytophthora parasitica* in green tomato fruit sampled at hourly intervals after the onset of an irrigation of soils previously irrigated every 4, 8, 16, or 32 days for 64 days. Percentages represented by each data point were calculated by averaging the number of fruit infected by *P. parasitica* in four replications of 10 fruit each. LSD = 21.9 at  $P = 0.05$ .

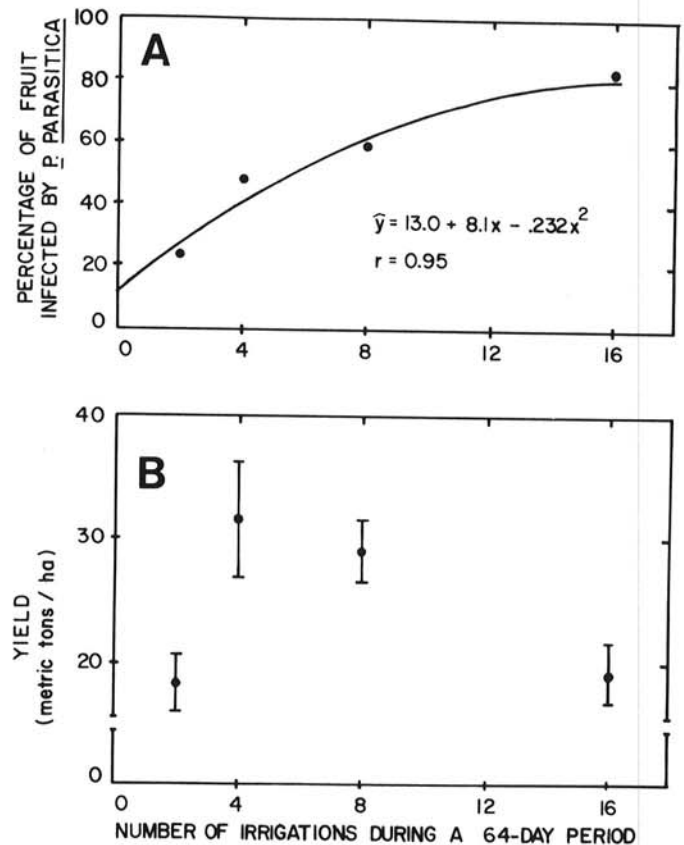


Fig. 3. Effect of long-term variations in irrigation frequency on the incidence of buckeye rot caused by *Phytophthora parasitica* on green tomato fruit attached to the vines and on yield of healthy fruit. Disease incidence and yield were evaluated 13 days after a final irrigation following 64 days in which furrows that were irrigated every 4, 8, 16, or 32 days received 16, 8, 4, or 2 irrigations, respectively. A, Each point represents the mean percentage of diseased fruit in four replications of an average of 192 fruit each. B, Points represent the mean weights of fruit harvested from four replications of 27 plants each, converted to metric tons per hectare. Vertical lines indicate standard deviations.

days, and infection during the flooding period ranged from 5 to 35% or from 15 to 30%, respectively. Cherry tomatoes were not infected until 4 hr after flooding in soils previously irrigated every 16 days and infection never exceeded 10%. There were no infections of control fruit or fruit floated over soils that had been irrigated every 32 days.

## DISCUSSION

Although the severity of *Phytophthora* root rots, including those of avocado (30) and safflower (31), is generally known to increase with increased frequency of irrigation, there are only a few published accounts (28,30,31) of the effects of irrigation schedule or technique on the development of diseases caused by soilborne *Phytophthora* spp. under field conditions. In one study (28) of irrigation effects in the field, the incidence of alfalfa root rot caused by *P. megasperma* f. sp. *medicaginis* was significantly greater in soils maintained continually or intermittently at  $\psi_m \geq -0.1$  bar than when irrigation was withheld or when the onset of a regular irrigation schedule was delayed 6 wk. In the present study, frequent irrigation resulted in an increase in both the final incidence of buckeye rot on fruit grown in the field (Fig. 3A) and the rate and incidence of infection during single irrigations late in the season (Figs. 1 and 2). Soils remained more moist in the frequently irrigated treatments, not only because the time interval between irrigations was relatively short, but also because the total volume of water applied increased with the frequency of irrigation. The highly significant correlation between increased frequency of irrigation during crop growth and increased final incidence of disease suggests that more frequent periods of soil saturation and more moist soil conditions between saturated periods enhance the reproduction, growth, and survival of *P. parasitica*.

Several researchers have examined some of the influences of soil moisture on the behavior of *P. parasitica*. Of the propagules produced by *P. parasitica*, the effects of soil moisture are best known for chlamydospores and sporangia. Holdaway (10) found chlamydospores of *P. parasitica* to survive longest in soil at  $\sim -500$  mb  $\psi_m$ , and Feld (7) reported that some chlamydospores may survive 7 days in soils as moist as 0 to  $-50$  mb  $\psi_m$ . Sporangium production by *P. parasitica* may occur at  $\psi_m$  values between  $-50$  and  $-700$  mb (7), and if the fungus is first incubated in soil at  $-200$  to  $-300$  mb  $\psi_m$ , sporangia may form abundantly when the soil becomes saturated (2). In the present study, in soils of furrows irrigated every 4 or 8 days,  $\psi_m$  remained higher than  $\sim -800$  mb and, therefore,  $\psi_m$  was conceivably high enough for some chlamydospores and sporangia to effectively persist from one irrigation to the next. One study (7) of the survival of *P. parasitica* in a citrus grove demonstrated that the number of propagules produced in furrow-irrigated soils that fluctuated between 0 and

$-150$  mb  $\psi_m$  (30 cm from the furrow center) was significantly greater than in drip-irrigated soils in which  $\psi_m$  ranged from  $-50$  to  $-300$  mb (30 cm from the emitter). As was noted above, a  $\psi_m$  value of zero may stimulate *P. parasitica* to form sporangia (2). Furthermore, in all *Phytophthora* spp. that have been examined, raising the  $\psi_m$  value to zero stimulates zoospore release (2,7) and aids zoospore dispersal (6). Because soil  $\psi_m$  was raised to zero during irrigations, it seems very likely that during the present study the release and effective dispersal of zoospores of *P. parasitica* to tomato fruit, or to other substrates on which growth and sporulation subsequently occurred, increased with the number of irrigations applied during crop growth. In contrast, irrigations separated by 16 or 32 days allowed the upper layers of soil to dry to  $\Psi$  values as low as  $-26$  and  $-63$  bars, respectively, which might affect the survival of *P. parasitica* adversely.

When soil samples collected 4 or 8 days after irrigation were enclosed in mesh with  $10\text{-}\mu\text{m}$  openings and flooded, cherry tomato baits were infected within 25 min, whereas relatively few fruit were infected when floated over soils collected 16 or 32 days after irrigation. The fact that zoospores, but not other propagules of *P. parasitica*, are capable of passing through the mesh provides evidence that zoospores were the propagules that caused infections within 25 min after the onset of flooding in moist soils. In addition, infections occurred in the field within 1 hr after the onset of irrigation in furrows previously irrigated every 4 or 8 days, whereas 3 or 5 hr were required for first infections in furrows irrigated every 16 or 32 days (Fig. 2). Although the exact behavior of *P. parasitica* under the conditions reported here is unknown, these results suggest that zoospores were released more promptly after the onset of final irrigations in the frequently irrigated treatments. The most likely source of the zoospores released shortly after the onset of irrigation would probably be sporangia that were already present, because new sporangium production by *P. parasitica* may require at least 4 hr (1). Also, cysts of some *Phytophthora* species (15,16) can persist in soil under the conditions reported here for frequently irrigated furrows, and zoospore cysts of *P. parasitica* and microsporangia formed by them are reported to release zoospores (4,23). Chlamydospores and oospores, which germinate primarily by formation of a germ tube and sporangium (25), represent other possible sources of zoospores. However, it is unlikely that these propagules could produce zoospores within 25 min. Finally, the absence of prompt infections after the flooding of drier soils suggests that zoospores were present in appreciable numbers only after enough time had passed for germination and sporangium production by propagules that survive in dry soils.

The data presented here demonstrate that irrigations that apply water to fields for long periods of time result in high levels of buckeye rot (Figs. 1 and 2). However, in many commercial fields it is not possible to avoid disease by reducing the length of individual irrigations. Furrows 300–400 m long in many commercial fields necessitate irrigations of at least 4–5 hr, and 8- to 10-hr irrigations are not uncommon. Even after the application of irrigation water ceases, fruit infections by zoospores will continue to occur until the soil drains to  $\psi_m$  values that limit zoospore release (2) and motility (6). The period required for soils to drain after irrigation to  $\psi_m$  values that limit infection may be prolonged in commercial tomato fields of the San Joaquin Valley where the rate of water penetration into the soil profile can be very slow (12), much slower than in the field plot at Davis. A reduction in the frequency of irrigation, which currently may be as often as every 5–8 days in commercial fields, may provide a more practical and successful means of avoiding the disease. Reductions in irrigation frequency could be accomplished by changing irrigation schedules or by alternate irrigation of every other furrow, and such reductions should contribute to increased yield of healthy fruit (Fig. 3B). Less frequent irrigation could be particularly effective in the fall, when cool temperatures result in prolonged periods of high soil moisture and buckeye rot has traditionally caused the greatest reductions in yield.

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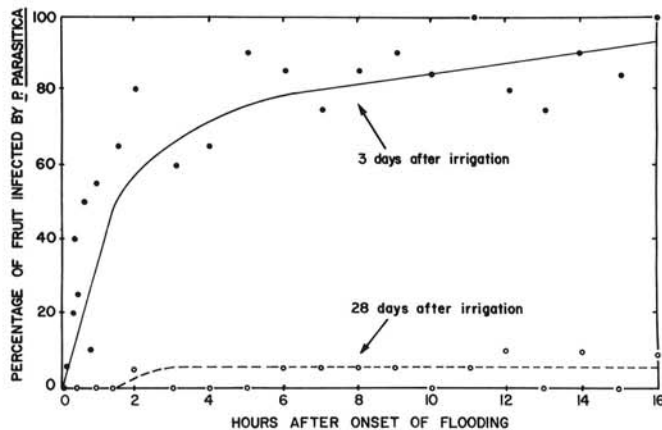


Fig. 4. Influence of the extent of prior soil drying on infection of cherry tomato fruit by *Phytophthora parasitica* during flooding. Fruit were floated for various time intervals over flooded soils collected from field plots that had not been irrigated for 3 or 28 days. Before flooding in the laboratory the water potentials ( $\Psi$ ) of the soils collected from the two irrigation treatments averaged  $-1.9 \pm 0.7$  and  $-219 \pm 48$  bars.

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