Reprinted from Vol. 114(4), July 1989
*Journal of the American Society for Horticultural Science*
Alexandria, VA 22314

J. Amer. Soc. Hort. Sci. 114(4):556–561. 1989.

# Phytophthora Root Rot and Irrigation Schedule Influence Growth and Phenology of Processing Tomatoes

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*Additional index words.* disease epidemiology, *Lycopersicon esculentum,* crop loss assessment, yield, partitioning

***Abstract.*** **Processing tomatoes (*Lycopersicon esculentum* Mill.) grown in field plots with soil infested or not infested with *Phytophthora parasitica* Dastur. were furrow-irrigated for 4 to 8 hr every 14 days (normal) or 28 days (less frequent) or with alternating 4- to 8-hr and 24-hr irrigations every 14 days (prolonged). Disease developed more rapidly and symptom severity was significantly greater on shoots and roots of plants that received prolonged irrigations. Disease symptoms on roots progressed more rapidly and were observed earlier than those on shoots in plants given prolonged or normal irrigation. Severe disease during early vegetative and reproductive growth caused significant reductions in total plant, leaf, and fruit dry matter and in the numbers of flowers and fruit in plants receiving either prolonged or normal irrigation. Diseased plants given prolonged irrigation also partitioned less total dry matter into leaves and fruit and more into stems than noninoculated plants. Less frequent irrigation of infested plots caused a delay in disease onset and reduced the impact of disease on numbers of flowers, fruit, and dry matter accumulation. Phytophthora-induced water stress during critical stages of crop development apparently can have major impacts on plant growth, phenology, and yield in processing tomato.**

Phytophthora root rot, caused by *Phytophthora parasitica,* is a major disease of processing tomatoes under irrigated conditions in California. A previous study showed that the frequency and duration of furrow irrigations can have large effects on both disease progress and yield in processing tomatoes (17); however, little is known about the impact of phytophthora root rot on specific stages of crop development that contribute to harvestable yield in tomato.

Specific stages of crop development are known to be sensitive to diseases caused by other soilborne plant pathogens; e.g., *P. megasperma* f. sp. *glycinea* and *Rhizoctonia solani* affect yield primarily through a reduction in plant stand (23, 24). Disease incited by *R. solani* also can lengthen the period of time to flowering and podset in dry bean (24). *Verticillium dahliae* causes major yield reductions in cotton by reducing plant height, lateral branching of stems, and net dry matter accumulation (16). However, with most soilborne pathogens, including *Phytophthora* spp., more quantitative information needs to be developed to describe impacts of root diseases on crop growth for inclusion in crop simulation models and to effectively predict yield losses (3, 7).

Root rots incited by *Phytophthora* spp. are known to cause reductions in leaf water potential by increasing resistance to water uptake through roots and stems (5, 8, 13). Vegetative and reproductive growth of plants can be extremely sensitive to water stress (1, 10, 20), and water stress during critical periods of crop development can have adverse effects on crop growth and yield (20). In tomato, flower bud abortion is increased by water stress and the length of the fruit growth period and total yield can be reduced (1, 19). Fruit ripening and total soluble solids concentration in individual fruit are generally increased by water

Received for publication 8 Aug. 1988. This research was supported in part by the Univ. of California Statewide Integrated Pest Management Project. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

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stress since total assimilates are transported to fewer fruit (4, 14).

The effects of phytophthora-induced water stress on yield components of processing tomatoes have not been previously examined. The objective of this research was to evaluate the influence of variation in irrigation regime on phytophthora root rot development and subsequent effects on the growth and phenology of processing tomatoes in the field. A summary of a portion of this work has been published (2).

## Materials and Methods

The measurements reported here were part of a 1986 field experiment conducted at the Univ. of California, Davis, for which many of the methods have been described (17). The processing tomato cultivar Ferry Morse 6203 was planted in single-row beds (1.5 m between furrow centers) with recommended cultural practices (1). The field did not initially contain detectable levels of *P. parasitica* Dastur, as indicated by soil dilution plating. Therefore, half of the plots were artificially infested with a mixture of five isolates of the pathogen 42 days after planting. All furrows were then immediately irrigated for 4 hr. Subsequent irrigations were started 2 weeks later and applied differentially among treatments arranged in a split-plot design with inoculum vs. no inoculum as the main plots and irrigation regime as the subplots. In subplot 1, water was applied to furrows for 4 to 8 hr every 14 days (normal irrigation). In subplot 2, irrigations were applied as in subplot 1, except that alternate irrigations were extended to maintain water in the furrows for 24 hr (prolonged irrigation). In subplot 3, water was applied to furrows for 4 to 8 hr every 28 days (less frequent irrigation). Each treatment was replicated four times, and each subplot contained two parallel beds, each 13.7 m long with a single row of plants in each bed. Each row contained an average of 65 plants.

Plants in one bed were used to observe symptom development on shoots and for a final harvest of fruit (17). Plants were removed periodically and disease incidence and severity on shoots and roots were evaluated every 2 weeks from plants randomly sampled from the second bed of each subplot. All disease ratings, except those at 99 days after planting, which are not presented, were made by the same observer. The number of plants used for observations of symptoms on shoots in each unit ranged from 21 to 6 as sampling times progressed because samples were removed from the plots. Beds from which plants were sampled destructively were divided into eight quadrats. Three adjacent plants from a randomly assigned quadrat were sampled at each sampling time, leaving a border of three to four plants between sampling locations. At the time of sampling, shoot symptoms on all remaining plants were rated on a scale from 0 to 4 (0 = no foliar symptoms; 1 = general wilting of entire plant; 2 = severe foliar wilting and chlorosis of more than 25% of the foliage; 3 = wilting of main stem, 25% to 75% of foliage necrotic; 4 = greater than 75% of foliage necrotic, main stem necrotic). After shoot symptoms were evaluated, sampled plants were cut at ground level and large roots from the 0- to 30-cm depth were rated for root rot severity on a scale of 0 to 4 (0 = no root discoloration; 1 = less than 25% of lateral roots brown, no taproot browning; 2 = 26% to 50% of all lateral roots brown, less than 50% of taproot brown; 3 = 51% to 75% of all lateral roots brown, 51% to 75% of tap root brown; 4 = greater than 75% of all lateral and tap roots brown). Although data were recorded for individual plants, ratings of symptoms on shoots and roots of the same plant were made independently. The pathogen was consistently isolated from diseased root tissue on a selective medium (17). Yield components measured from destructively sampled plants were numbers of living, dead, or aborted flower buds and flowers, and numbers of fruits in various stages of development (B1 $\leq$ 2.5 cm, green; B2 > 2.5 cm, green; B3 = pink, immature; B4 = mature red). Total dry weight of leaves, stems, roots, and fruits was determined for each plant after drying at 60C.

Data are presented with the individual plant as the base unit; however, data can be converted to a land-area basis using the factor 2.86 plants/m$^2$. We performed correlation analysis and analysis of variance of the dry matter and phenology data from individual plants by time using SAS packages (21). Orthogonal contrasts were used to separate treatment means. Disease data from destructively sampled plots were analyzed separately from data collected from nondestructively sampled plots. Relative growth rates of plants during periods approximating exponential growth were calculated from the equation $dW/dt = RW$, where W is dry weight, t is time, and R is the relative growth rate (6). Integration gives $(\ln W_2 - \ln W_1) / (t_2 - t_1) = R$, where subscripts 1 and 2 refer to the time of measurement.

## Results

*Progression of disease symptoms.* In the destructively sampled plots, irrigation regime had significant effects on disease development. After the first uniform irrigation at 44 days after planting, symptoms became apparent on roots in all of the pathogen-infested plots (Fig. 1A). The subsequent increase in symptom development on roots was affected by irrigation regime. Symptom severity on roots of plants in infested plots given prolonged irrigation was significantly greater ($P \leq 0.5$) than symptom severity on roots of plants given the normal irrigation on the 14-day schedule at 70 and 84 days after planting. Symptom severity on roots of plants in infested plots irrigated less frequently was lower than in the other two treatments at 70, 84, 112, and 125 days after planting (Fig. 1A). Lesions advanced sooner in taproots of plants in infested plots given either prolonged or normal irrigation than in plants given less-frequent irrigation.

In destructively sampled plots, rapid increase in symptoms on shoots occurred in plants given prolonged or normal irrigations, but shoot symptoms occurred later (15 days) than root symptoms in these treatments (Fig. 1B). Symptoms on shoots of plants irrigated less frequently were not observed until after an irrigation was applied 77 days after planting (Fig. 1B). Severity of symptoms on roots was positively correlated ( $P \leq 0.0001$) with severity of symptoms of disease on shoots at 70, 84, 112, and 125 days after planting ($r$ = 0.69, 0.86, 0.93, and 0.95, respectively). No symptoms of disease developed in plants in noninfested plots.

*Numbers of flowers and fruit.* Peak numbers of flower buds (94 to 113 per plant) were observed 55 days after planting and were not greatly affected by disease. Flower numbers observed on plants at 70 days after planting were significantly ($P \leq 0.01$) affected by disease (Fig. 2A). Plants in infested plots given a prolonged irrigation early in the season had the lowest numbers of flowers at this time, while plants in infested plots irrigated on the 28-day schedule or plants in noninfested plots had more flowers (Fig. 2A). A significant ($P \leq 0.01$) negative correlation was found between disease symptoms on roots (Fig. 1A) and numbers of flowers ($r = -0.32$). In addition, more reproductive structures (flower buds, flowers, and fruit) were aborted in plants in infested plots given prolonged or normal irrigations

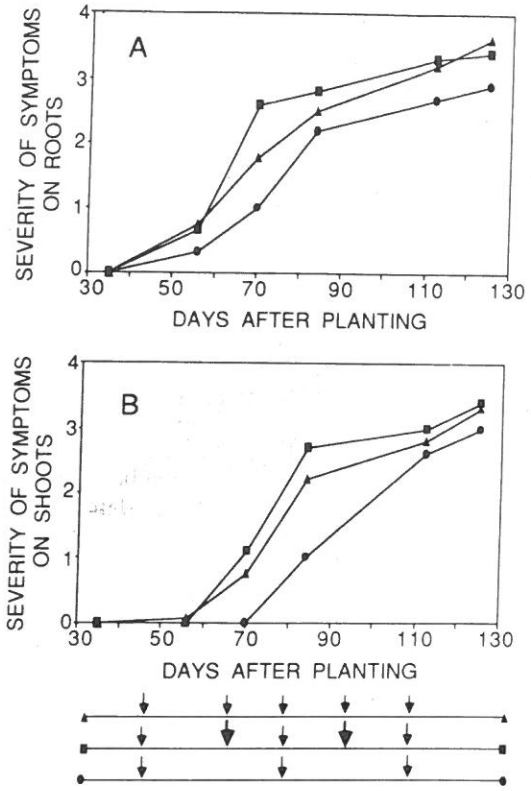


Fig. 1. Progression of phytophthora root rot symptoms on processing tomatoes in infested plots that were destructively sampled. (**A**) Severity of symptoms on roots; (**B**) Severity of symptoms on shoots. Symptoms were measured on a scale of 0 (no symptoms) to 4 (severe symptoms). Treatments were 4- to 8-hr irrigations at 14 (triangles; normal) or 28 days (circles; less frequent), or alternating 4- to 8-hr and 24-hr irrigations at 14 days (squares; prolonged). Heavy and light arrows beneath the figure indicate times of 24-hr and 4- to 8-hr irrigations, respectively. Number of samples per treatment was 21, 18, 15, 12, 9, and 6 at each progressive measurement time, respectively.

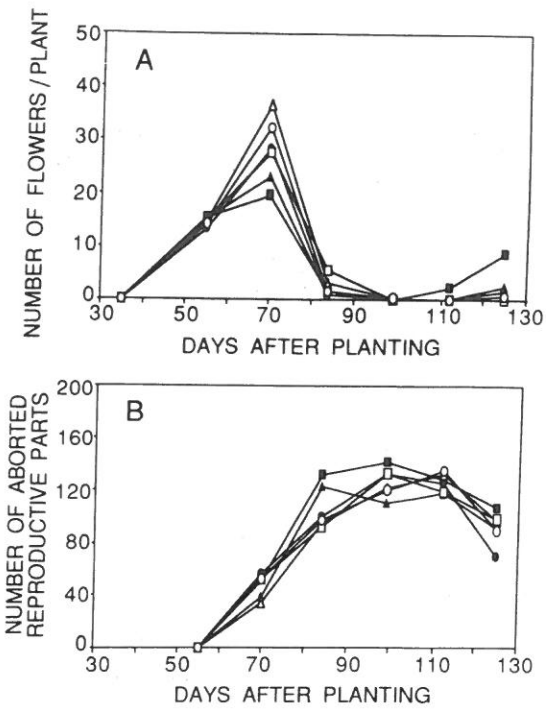


Fig. 2. (**A**) Number of flowers per plant. (**B**) Number of aborted reproductive parts (flower buds, flowers and/or fruit) per plant in processing tomatoes grown in *P. parasitica*-infested (closed symbols) or uninfested soil (open symbols). Irrigation treatments were 4- to 8-hr irrigations at 14 days (triangles; normal) or 28 days (circles; less frequent), or alternating 4- to 8-hr and 24-hr irrigations at 14 days (squares; prolonged).

than in other treatments by 84 days after planting (Fig. 2B), when symptom severity on shoots in these two treatments approached a maximum (Fig. 1B). The inoculum effect on abortion of reproductive structures was significant only at 84 days after planting. At 84 days after planting, a significant and positive correlation ($P \leq 0.0001$) was found between root rot severity and numbers of dead flowers per plant ($r = 0.42$). Late in the season, flowering resumed to a limited extent in severely diseased plants given the prolonged irrigation (Fig. 2A).

Reduced flower numbers affected subsequent fruiting in all stages of fruit development (Fig. 3). Plants in infested plots given prolonged irrigations had fewer flowers and formed fewer B1, B2, and B4 fruits than did plants in infested plots irrigated on the less-frequent 28-day schedule. The B3 (pink) stage was brief and data are not shown. Numbers of mature red fruit (B4) were reduced by 50% at harvest in plants in infested plots given prolonged irrigations compared with noninfested controls on the same irrigation schedule (Fig. 3C). The inoculum by irrigation interaction on numbers of fruit was significant ($P \leq 0.01$) for B1, B2, and B4 fruit at 70, 84, and 125 days after planting, respectively.

*Dry matter production and partitioning.* Leaf dry matter was reduced significantly ($P \leq 0.05$) by disease when measured at 84, 99, 112, and 125 days after planting for each irrigation schedule (Fig. 4A). Disease reduced dry matter production of leaves between 55 and 84 days after planting in plants in infested plots irrigated on the 14-day schedule and between 70 and 84 days after planting in plants in infested plots irrigated on the 28-day schedule. Relative growth rates of plants in infested plots were also reduced during these time periods (data not shown). Leaves of plants in noninfested plots accumulated significantly greater amounts of dry matter and had uniformly more relative growth than diseased plants regardless of irrigation schedule. Significant ($P \leq 0.01$) negative correlations were found between the severity ratings on roots and leaf dry weight at 70, 84, 112, and 125 days after planting ($r = -0.30$, $-0.43$, $-0.42$, and $-0.58$, respectively), and between disease ratings on shoots and leaf dry weight at 84, 112, and 125 days after planting ($r = -0.44$, $-0.42$, and $-0.58$, respectively). Stem dry matter accounted for up to 30% of total plant dry matter at most sampling times during the season. Stem dry matter was not significantly reduced by disease at any sampling time, although diseased plants irrigated on the 14-day schedule had lower stem dry weights at harvest (Fig. 4B). No significant differences in root dry weights were obtained. Dry weights of roots recovered ranged from <1 to 6 to 9 g/plant as the season progressed, and represented a small percentage of total plant weights. Therefore, the root weights obtained probably do not represent a meaningful sample of the entire root mass in soil.

Plants in infested plots given prolonged irrigations had significantly less fruit dry matter at 99 days after planting, whereas plants in infested plots irrigated less frequently or normally did not differ significantly from plants in noninfested plots in fruit dry matter production (Fig. 4C). In comparison with other treat-

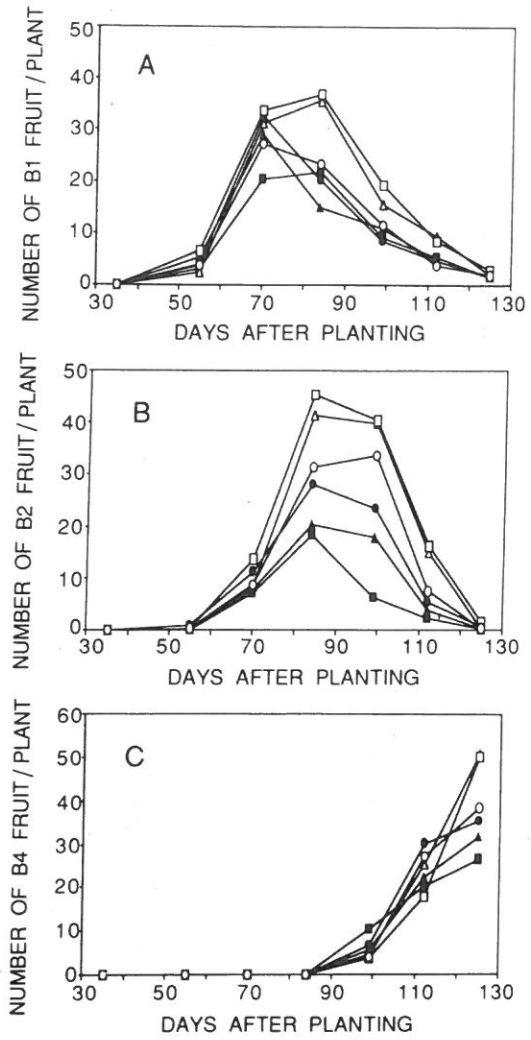


Fig. 3. Numbers of fruit in various stages of development per plant in processing tomatoes grown in *P. parasitica*-infested (closed symbols) or uninfested soil (open symbols). (**A**) B1 = green fruit ≤2.5 cm in diameter. (**B**) B2 = green fruit >2.5 cm in diameter. (**C**) B4 = mature red fruit. Irrigation treatments were 4- to 8-hr irrigations at 14 (triangles; normal) or 28 days (circles; less frequent), or alternating 4- to 8-hr and 24-hr irrigations at 14 days (squares; prolonged).

ments, there was little increase in fruit dry weight between 84 days after planting and harvest in plants in infested plots given prolonged irrigation. Plants in noninfested plots and plants in infested plots irrigated less frequently or normally continued to partition dry weight into fruits until 112 days after planting, after which time reductions in fruit dry weight were observed in most of the treatments and probably were due to fruit ripening (Fig. 4C).

Disease and irrigation also affected fruit ripening in tomato. In noninfested plots, increased irrigation frequency delayed ripening, whereas, in infested plots, more frequent irrigation and severe disease tended to accelerate ripening. At harvest, significant ($P \leq 0.0001$) negative relationships were found between the final severity of symptoms on roots ($r = -0.51$) or shoots ($r = -0.53$) and fruit dry weight. Total dry matter at harvest (a composite of leaf, stem, root, and fruit dry matter) was reduced significantly by disease in infested plots with greatest reductions in plants in infested plots irrigated on the 14-day schedule (Fig. 4D). Total plant dry matter also was negatively correlated with final symptom severity on roots and shoots ($r = -0.54$ and $-0.55$).

In plants in noninfested plots irrigated for 4 to 8 hr on a 14-day schedule, leaves accounted for > 70% of the total aboveground dry matter at 36 days after planting (Fig. 5). The fraction of dry weight partitioned into leaves subsequently decreased, as there were progressively greater allocations of dry matter first to stems and later to fruit. Diseased plants given prolonged irrigations partitioned less total dry matter into leaves and more into stems during the period between 55 and 84 days after planting than plants in noninfested plots given normal irrigation (Fig. 5). These plants also allocated a lesser fraction of their dry weight to fruit between 84 days after planting and harvest (Fig. 5). Whereas only the largest differences in partitioning between infested and noninfested treatments are shown in Fig. 5, diseased plants given normal and less frequent irrigations also partitioned less total dry matter into leaves and more into stems between 55 days after planting and harvest than did healthy plants. Harvest index (ratio of harvestable fruit dry weight to total aboveground dry weight) was reduced from 0.48 in plants in noninfested plots irrigated for 4 to 8 hr on the 14-day schedule to 0.39 in plants in infested plots given prolonged irrigations. Harvest indices were less affected in plants in infested plots given normal or less frequent irrigations when compared with similarly irrigated noninfested controls.

## Discussion

Variations in the schedule of furrow irrigation and resulting variations in the development of phytophthora root rot had major impacts on growth and phenology in processing tomatoes. The most severe root and shoot disease symptoms, and greatest reduction in growth, occurred in plants in infested plots given prolonged irrigations (Fig. 1). On the other hand, the onset of disease symptoms on shoots was delayed and growth reduction caused by disease was less when infested plots were irrigated less frequently. Disease symptoms on roots were more severe than symptoms on shoots early in the season, and visible symptoms did not develop on shoots until severities of symptoms on roots exceeded a rating or 1.7 (Fig. 1). Evidently, a critical amount of infection on lateral and taproots in the top 30 cm of soil may be required for shoot symptoms to develop. While the effects of irrigation schedule on disease development reported here are significant (Fig. 1), the same irrigation treatments can have even larger effects on phytophthora root rot development in shoots of processing tomatoes (17).

Reductions in vegetative growth caused by phytophthora root rot (Fig. 4) are probably due in large part to water stress. Various phytophthora root rots have been shown to induce water stress (7, 8, 13), and measurements reported previously (17) have shown clearly that phytophthora root rot reduced leaf water potential. Leaf dry matter was reduced by disease in all infested plots, but reductions were greater in diseased plants irrigated on a 14- rather than a 28-day schedule (Fig. 4). Because disease was delayed in plants irrigated on the less-frequent schedule, leaf water potential remained higher during the early exponential phase of vegetative growth. Therefore, vegetative growth was less affected by disease-induced water stress in this treatment. Vegetative growth in processing tomatoes is extremely sensitive to small reductions in leaf water potential (12, 15); these results suggest that, while other mechanisms may also be involved, vegetative growth was reduced by phytophthora-induced water stress. The development of resistant tomato cultivars that are

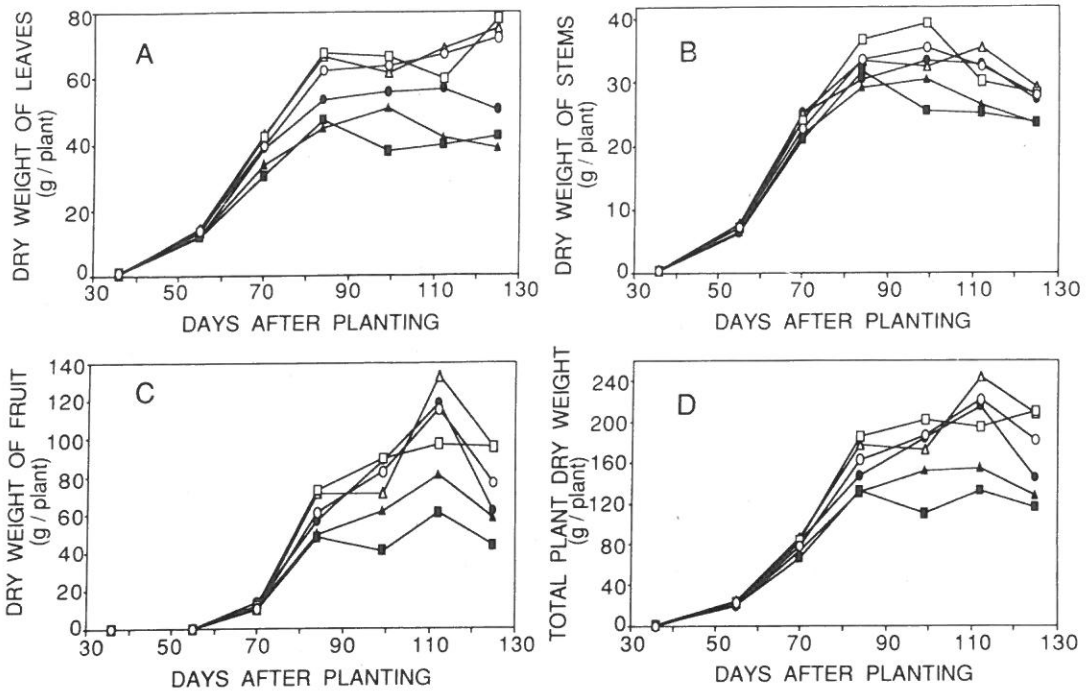


Fig. 4. Dry matter accumulation in processing tomato grown in *P. parasitica*-infested (closed symbols) or uninfested soil (open symbols). (**A**) Leaves. (**B**) Stems. (**C**) Fruit. (**D**) Total plant. Irrigation treatments were 4- to 8-hr irrigations at 14 days (triangles; normal) or 28 days (circles; less frequent), or alternating 4- to 8-hr and 24-hr irrigations at 14 days (squares; prolonged).

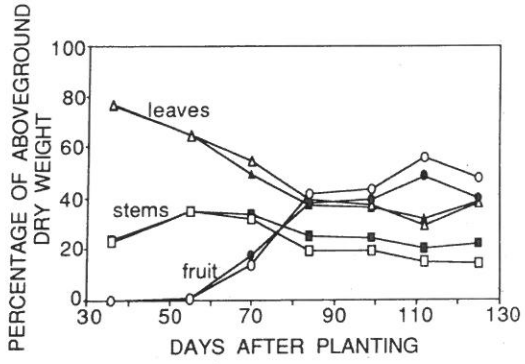


Fig. 5. Partitioning of aboveground dry matter between leaves (triangles), stems (squares), and fruits (circles) of tomato plants in *P. parasitica*-infested soil given alternate 4- to 8-hr and 24-hr irrigations at 14 days (closed symbols), and uninfested soil given 4- to 8-hr irrigations on a 14-day schedule (open symbols).

able to develop more extensive root systems early in the season and maintain higher plant-leaf water potentials under disease pressure may alleviate some of the detrimental impacts of *P. parasitica* on host growth and yield.

Processing tomato cultivars are determinate and produce a prolific number of flowers followed by a period when fruit growth is dominant (1). Yield in processing tomato is derived largely from inflorescences that blossom in the first 15 days of flowering (18). This synchrony in fruiting has made machine harvesting possible. Thus, reductions in numbers of flowers and fruit set early in the flowering period, as occurred in the more severely diseased plants, significantly decreased numbers of fruit finally contributing to yield (Fig. 3C). Since fewer fruit formed, less total dry matter was partitioned to fruit in severely diseased plants. Also, the length of time dry matter was partitioned to fruit was reduced in severely diseased plants (Fig. 4C). There was little increase in fruit dry weight between 84 days after planting and harvest in plants in infested plots given prolonged irrigations, whereas noninfested control plants and plants in infested plots irrigated less frequently continued to partition dry matter to fruit until 112 days after planting (Fig. 4C). Also, a greater percentage of the fruit on diseased plants was set early. Although these fruit contributed to final yield, a greater percentage of them matured early and were of lower quality. It is clear that disease effects on yield can be high during early phases of reproductive growth, which are critical in crop development.

Previous studies have shown that reproductive growth in processing tomato is highly correlated with vegetative growth and that vegetative growth is more sensitive to water stress than reproductive growth (12, 15). Since vegetative growth was severely reduced by disease (Fig. 4), the reductions in numbers of flowers observed in diseased plants could have been due to this reduced growth. The maximum adverse effect of disease on flowering was observed 70 days after planting, when shoot symptoms were mild but root symptoms were increasing rapidly (Fig. 1) and leaf growth was decreased significantly (Fig. 4A). In fact, the numbers of flower buds formed on plants at 36, 55, and 70 days after planting were positively correlated with leaf dry matter ($r$ = 0.60, 0.71, and 0.56). It has been shown that numbers of inflorescences are reduced in processing tomatoes with leaf water potentials only 3 bars lower than well-irrigated controls (12). Since water stress inhibits growth of vegetative shoot apices, the formation of new flower buds is reduced and the reproductive growth period is shortened (12).

Severely diseased plants not only produced fewer reproductive structures, they also aborted more reproductive parts (Fig. 2B). These results differ from those of Nyabundi (15), who showed that tomato plants subjected to mild water stress retained a greater number of flowers early in the season and partitioned

a higher proportion of total aboveground dry matter to fruit than did well-irrigated controls. In contrast, phytophthora-infected plants in our study underwent severe water stress and partitioned less total biomass to fruit. The difference between the two studies may have resulted from the more severe water stress induced by disease than was induced in tomatoes by withholding irrigations in the previous experiments (15). Also, pathogen-induced changes in host physiology could have led to alterations in plant hormone levels, which may have affected reproductive growth and retention of flowers (25). Flower bud formation and renewed flowering occurred late in the season in severely diseased plants, especially those given prolonged irrigations (Fig. 2). These reproductive structures, however, were formed too late to contribute to harvestable yield. The resurgence in reproductive growth did not occur in plants in noninfested plots. Tomato fruit are a major sink for photosynthates, and grow at the expense of vegetative components and new reproductive structures (11, 19). Reduced fruit production in severely diseased plants reduced the sink created by fruit growth; therefore, assimilates may have been available for renewed vegetative and reproductive growth late in the season.

Root growth in tomato is determined partially by the amount of intersink competition for assimilate within the plant (9, 11, 19). Young plants partition assimilate from lower leaves to roots during early vegetative growth (22). When fruiting begins, assimilate translocation is reduced to roots and increased to fruits. Studies with indeterminate tomato cultivars have shown that, as soon as fruiting begins, significant root death occurs (11, 19). In our study, the period of most rapid fruit growth (Fig. 4C) coincided with a period of rapid increase in disease severity (Fig. 1). Competition for assimilates from developing fruit may have slowed new root growth or made existing roots more susceptible to infection by *P. parasitica* (9). Thus, reduced allocation of photosynthates to roots during fruit development may have reduced the ability of phytophthora-infected plants to resist invasion and/or compensate for loss of functional roots to disease.

Prolonged irrigation of plants in phytophthora-infested plots early in the season resulted in rapid disease development, whereas a delay in disease onset in shoots was observed in plants in infested plots irrigated less frequently in the experiment reported here and previously (17). The time of onset and duration of stress induced by *P. parasitica* had large impacts on critical stages of growth in processing tomatoes. Severe disease during early vegetative and reproductive growth reduced aboveground leaf dry matter, numbers of flowers, fruit set and, ultimately, final yield.

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