Relationships Among Phytophthora Root Rot Development, *P. parasitica* Populations in Soil, and Yield of Tomatoes Under Commercial Field Conditions

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ABSTRACT

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In 1989, 1990, and 1991, 6-m-long row segments of tomato cultivar FM6203 were planted adjacent to 10 other cultivars in 12 commercial fields (within 28 km of Davis, California) with histories of Phytophthora root rot. Populations of *Phytophthora parasitica* at planting ranged from 0 to 3.7 cfu/g of dry soil as determined by dilution plating, and 2–100% of tomato leaf disks used as bait in a soil assay were colonized. Populations increased and fluctuated during the growing season. Aboveground symptoms of disease developed at similar phenological stages, associated with the setting and maturation of fruit, in all cultivars, and the final disease incidence and severity ranged from zero to the maximum possible. Harvestable fruit yield decreased linearly with increased symptom severity for all cultivars and years. Final disease severity was correlated positively with pathogen populations detected by baiting at planting and with increasing soil clay content, and negatively with soil sand content and time after planting at which symptoms first became visible. There were no clear associations between pathogen populations and soil temperature or moisture. The results suggest that there is little difference among processing tomato cultivars in tolerance or yield potential under given levels of disease pressure.

Additional keywords: epidemiology, inoculum level, *Lycopersicon esculentum*, path coefficient analysis

Phytophthora root rot of processing tomatoes (*Lycopersicon esculentum* Mill.) in northern California is caused principally by *Phytophthora parasitica* Dastur (20), and previous studies showed that inoculum levels of *P. parasitica* used to infest tomato fields at 35 or 42 days after planting had significant effects on epidemic development and yield loss (13). Those results suggested that there may be an inoculum threshold for yield loss between 0.3 and 15 propagules per gram of dry soil, measured 35 or 42 days after planting, below which disease does not cause yield loss and above which disease may cause yield loss of a magnitude that varies with irrigation practices and other conditions.

Inoculum levels of *Phytophthora* spp. in field soils with a history of Phytophthora root rot are generally low or undetectable when soil is sampled before planting and increase in association with the development of disease symptoms on perennial hosts (4,7,10,11,23,25). In containers, inoculum levels of *Phytophthora* spp. as low as 10 and 50 chlamydospores per kilogram of soil are capable of initiating disease in Fraser fir (23) and tobacco plants (6), respectively. Field populations of *P. parasitica* in association with citrus roots were not detectable during winter months, increased in the spring, and reached maximum levels in midsummer (4). Chlamydospores were the primary overwintering propagule of *P. parasitica* near citrus roots (10). Few studies have quantified relationships between inoculum level of soilborne *Phytophthora* spp. that have the potential to cause multiple cycles of disease and epidemic development under natural field conditions (4,5,10,11,25), even though such relationships may be important for annual crops. Within annual crops, numbers of pathogen cycles may be limited, and perhaps those cycles early in a growing season have more effect on final disease severity and crop yield than cycles later in a growing season.

The objective of this study was to quantify relationships among inoculum level, epidemic development, and crop yield in commercial processing tomato fields with a known history of Phytophthora root rot and naturally infested with *P. parasitica*. Soil properties thought to influence Phytophthora root rot epidemics also were measured and related to epidemic development and crop yield.

MATERIALS AND METHODS

Experiments were conducted in 12 different commercial fields (four each in 1989, 1990, and 1991) of processing tomatoes in Yolo and Solano counties (within 28 km of Davis, California) with known histories of Phytophthora root rot on tomato. *P. parasitica* was detected in all experimental sites before planting by baiting nondiluted soil with tomato leaf disks (12). Numerous segments of 6-m-long rows, planted on beds with 1.5 m between bed centers, were used as experimental units in each field. Plants within experimental units, as well as those beyond both ends of row segments and in neighboring rows, were thinned to clumps of two to four plants per 20 cm of row 29–41 days after planting. To compare cultivars, experimental units were always paired; one unit was seeded directly to the reference cultivar FM6203 and the other unit, on an adjacent bed, was seeded directly to the grower's commercial cultivar in March and April of each year. Single or double-row beds were used depending on individual grower practices. Experimental units were located approximately 35 m from the low end of each field in areas where Phytophthora root rot had been evident previously. In fields where metalaxyl was used during the study period, it was withheld from areas encompassing the experimental plots. Fields were furrow-irrigated, with the exceptions of one field in 1989, three fields in 1990, and one field

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in 1991 in which a combination of sprinkler and furrow irrigations was used. The crop was managed according to standard grower practices. A total of 11 commercial cultivars, including FM6203, and 80 total experimental units were used in data analysis (Table 1). Several plots were started but dropped from the study for various reasons, including other confounding root pathogens, unusual management practices, or mechanical harvesting of the field before final data were collected.

Quantification of inoculum in soil. Pathogen populations were quantified by dilution plating at planting, thinning, and successive alternate weeks in experimental units of most cultivars. At planting, pathogen populations were quantified on a selective medium (6) amended with 72 μg/ml of hymexazol (Tachigaren 70WP) and baiting nondiluted soil with tomato leaf disk baits that were plated on selective medium; only the dilution plate assay was employed during the growing season. The specific methods used for both assays were described previously (12). Dilution plates and leaf bait methods had approximate detection thresholds of 3 and 0.4 cfu/g of dry soil, respectively (12). Populations were estimated for one composite sample of seven soil cores (1.9 cm in diameter and 25 cm deep) per experimental unit collected by sampling the entire width and length of the bed in a stratified random sampling pattern, collecting successive cores on alternating sides of the plant row.

Epidemic development and plant growth. Incidence of symptoms on shoots was quantified at least every 14 days and more frequently during rapid phases of epidemic development in most cultivars (Table 1). At crop maturity, severity of symptoms on shoots and roots and crop yield were measured for all cultivars. Severity of shoot and root symptoms was quantified on a scale of 0–4, where 0 = healthy, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100% of the shoot or root system affected. On shoots, wilting was generally apparent in plants with a rating of 1 or 2 and chlorosis and/or necrosis was visible for plants with a rating of 3 or 4. Lesions on fine and lateral roots were rated as 1 and 2, respectively, and lesions on lower and upper portions of the taproot were rated as 3 and 4, respectively.

At crop maturity, fresh weights of red fruit that were unblemished, had less than 50% sunburn, or had minor blossom end rot were added for each experimental unit to obtain a measure of harvestable yield comparable to that obtained in commercial production.

Soil temperatures and matric potentials were measured with thermistors and gypsum blocks 15 cm deep in the center of beds with DP222 Datapods (Omnidata International, Logan, UT). Soil temperature and matric potential were measured every 5 min, and hourly means were recorded. Soil moisture readings were transformed to soil matric potential (MPa) using a cubic regression equation from an empirical calibration of the gypsum blocks on a pressure plate (J. B. Ristaino, *personal communication*). Soil temperature and moisture were measured only for the last half of the season in the commercial fields because of standard cultivation practices. In 1989, additional soil properties likely to affect Phytophthora root rot, i.e., texture, cation exchange capacity, exchangeable sodium and calcium, chloride, electrical conductivity, and pH, were measured at the end of the season. Only soil texture and cation exchange capacity were measured in 1990 and 1991 because the other variables did not significantly affect disease development or yield loss in 1989. Soil analyses were performed by the Division of Agricultural and Natural Resources Analytical Laboratory at the University of California, Davis.

Statistical analyses. Linear relationships between pathogen populations at planting and final disease symptoms and between final disease symptoms and yield were determined by the regression procedure in SAS 6.04 (19). Effect of year on the slope and intercepts of significant linear models was tested by dummy variable regression (15,24). Regression coefficients were reported for 1989 as the base comparison, and the direction and magnitude of difference from the base comparison were reported for 1990 and 1991. All cultivars were pooled together for analysis because the regression line for the reference cultivar, FM6203, was parallel with the regression line of the combination of other commercial cultivars, indicating a similar effect of disease severity to yield reduction among cultivars.

Stepwise regression techniques and correlation coefficients were used to select variables of *P. parasitica* populations and development of disease symptoms associated with reduction in crop yield. Subsequently, the relationship between selected independent variables, i.e., soil sand content, soil clay content, time of epidemic initiation, proportion of leaf disks colonized, colony-forming units per gram determined by dilution plating, and final severity of disease

Table 1. Cultivars of processing tomatoes and numbers of experimental units of each cultivar during 1989, 1990, and 1991

Cultivar	Number of experimental units[a] 1989	1990	1991
FM6203	11	9	22
FM882	...	4	...
FM785	...	4	...
Asgrow Allegro	1[b]	...	...
Asgrow Brigade	...	4	6
Campbell Alta	1[b]	...	...
Del Monte 6796	...	...	3
HM 3075	...	...	6
Heinz 8561	1[b]	...	...
Heinz 2152	6[b]	...	...
Sun Seeds 1643	2[b]	...	...
Total	22	21	37

[a] As much as possible, each unit planted with the reference cultivar, FM6203, was located next to a unit planted by a grower with one of the other cultivars.
[b] Only final symptoms on shoots and roots and fruit yield were measured.

Table 2. Parameter estimates for linear regression equations using dummy variables[a] comparing the proportion of leaf disks colonized by *Phytophthora parasitica* at planting to final severity of Phytophthora root rot for 12 commercial field locations and seven commercial processing tomato cultivars during 1989–1991

Variables in regression[b] Year	Depend.	Indep.	Regression parameter	Parameter estimate[c]	SD[d]	Between years *P*
1989	Shoot	%Leaf	Intercept	−1.159	1.308	
1990	Shoot	%Leaf	Intercept	1.415	1.341	0.0084
1991	Shoot	%Leaf	Intercept	0.675	1.449	
1989	Shoot	%Leaf	Slope	4.215	1.593	
1990	Shoot	%Leaf	Slope	−2.040	1.696	0.4583
1991	Shoot	%Leaf	Slope	−2.121	1.734	
1989	Root	%Leaf	Intercept	−1.966	1.215	
1990	Root	%Leaf	Intercept	1.946	1.245	0.0056
1991	Root	%Leaf	Intercept	0.637	1.346	
1989	Root	%Leaf	Slope	4.345	1.479	
1990	Root	%Leaf	Slope	−2.467	1.575	0.2830
1991	Root	%Leaf	Slope	−1.885	1.611	

[a] $R^2 = 0.4126$ for the linear model Shoot = f(%Leaf); $R^2 = 0.4253$ for the linear model Root = f(%Leaf).
[b] Shoot and Root were mean disease severities (0–4) for shoots and roots, respectively, for all plants in 6-m-long row segments, and %Leaf was the proportion of leaf disks colonized by *P. parasitica* on saturated soil sampled at the time of planting.
[c] The parameters for 1989 are as shown, but the parameters for 1990 and 1991 must be added to the 1989 parameter to determine the actual value for each year. All parameters were estimated with a single degree of freedom.
[d] Standard error for the parameter estimate; the actual value for each year is shown.

symptoms, with one another and to the dependent variable, i.e., crop yield, were analyzed by path coefficient analysis (3,9). Percent soil sand and clay contents were transformed as $\ln(x)$ before analysis to normalize the data. Data were analyzed with the stepwise, correlation, and regression procedures of SAS 6.04 (19).

RESULTS

Initial populations of *P. parasitica* measured at planting ranged from 0 to 3.7 cfu/g, and 2–100% (median = 92%) of the leaf disks were colonized. Isolates from all fields were found to be pathogenic to tomato seedlings (*unpublished*). Soil populations fluctuated considerably throughout the growing season. For example, the median differences between maximum population levels during the growing season and populations at the time of planting were 48.0, 43.9, and 19.8 cfu/g for 1989, 1990, and 1991, respectively; the median difference across all 3 yr was 31.6 cfu/g. The peak populations occurred 108 ± 24 (mean ± standard deviation) days after planting, which on average was slightly before symptoms first became apparent on shoots at 118 ± 22 days after planting.

In many experimental units, symptoms became severe on shoots, yet populations of *P. parasitica* were not detectable by dilution plating at the time of planting. However, *P. parasitica* was detected in all experimental units by baiting soil with tomato leaf disks before and at planting. There was no significant correlation between dilution plating and baiting methods for quantification of pathogen populations ($P = 0.1888$). Although considerable variation existed, final severity of shoot and root symptoms increased significantly with increases in the proportion of leaf disks colonized by *P. parasitica* measured at planting (Table 2) but not with colony-forming units per gram determined by dilution plating (Fig. 1). Slope of the regression of final severity of shoot symptoms to proportion of colonized leaf disks did not differ significantly among years, but the intercepts of the lines were significantly different (Table 2).

Time of epidemic initiation (when first symptoms were visible) affected the final severity of shoot and root symptoms more than pathogen populations (Fig. 1). The shorter the period between planting and first appearance of symptoms, the more severe final symptoms became during the season. Severity of symptoms increased at the time of fruit setting and maturation. Fruit set occurred about 80–100 days after planting. Symptoms did not become visible on shoots unless the final severity of symptoms on roots was above a rating of 1 (lesions on fine roots); final severity of symptoms on shoots was positively correlated with the final severity of symptoms on roots (Fig. 2A, Table 3).

Harvestable yield was inversely related to the final severities of symptoms on shoots (Fig. 2B, Table 3) and roots (Fig. 2C, Table 3), with final shoot symptoms having a greater negative correlation with yield than root symptoms (Fig. 1). Average yield in experimental units without visible shoot symptoms was 34.2, 35.6, and 35.4 t/ha (30.8, 32.0, and 31.9 tons per acre) for 1989, 1990, and 1991, respectively, and the average across years was 35.0 t/ha. Average yield in experimental units with visible shoot symptoms was 21.0, 20.5, and 25.1 t/ha (18.9, 18.4, and 22.6 tons per acre) for 1989, 1990, and 1991, respectively, and average yield across years in plots with disease was 22.2 t/ha.

Sand content of soil affected populations of *P. parasitica* measured by dilution plating at planting and the time of initiation of disease development (Fig. 1), whereas other soil properties such as cation exchange capacity, exchangeable sodium and calcium, chloride, electrical conductivity, and pH did not. The relationships of soil clay and sand content to pathogen populations were more apparent when populations were measured at planting with dilution plating than by colonization of leaf disks (Fig. 1). Mean exchangeable sodium, exchangeable calcium, chloride, electrical

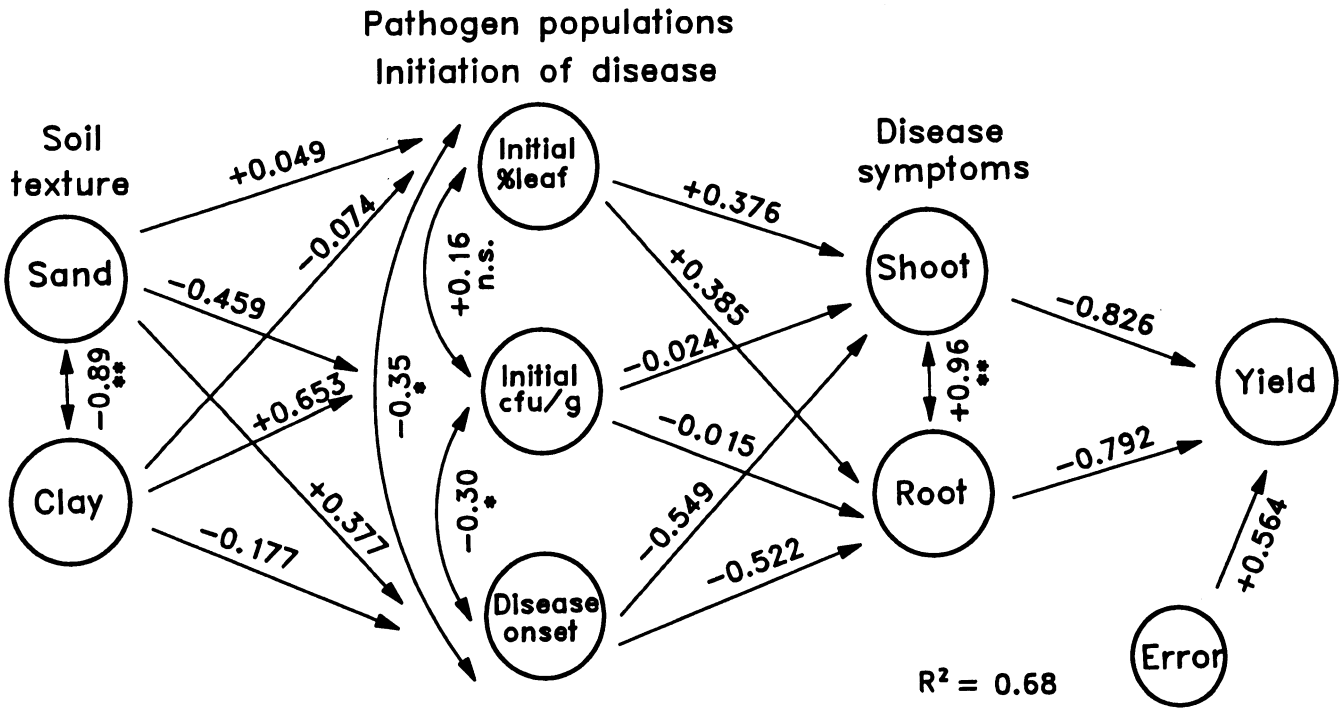

Fig. 1. Diagram of relationships examined by path coefficient analysis. Relationships between soil texture [ln (% soil sand content {Sand}) and ln (% soil clay content {Clay})], populations of *Phytophthora parasitica* at the time of planting, measured either as percent colonized leaf disks (Initial % leaf) or colony-forming units per gram from soil dilution plating (Initial cfu/g), time of epidemic initiation expressed as days after planting (Disease onset), final severity of symptoms (rated on scale of 0–4) on shoots (Shoot) and roots (Root), and crop yield in kilograms per experimental unit (Yield) for seven commercial processing tomato cultivars in 12 commercial fields during 1989, 1990, and 1991. The error component accounts for experimental error and variables not included in the model. The path coefficients are illustrated on single-headed arrows and linear correlation coefficients, on double-headed arrows. Absolute values of path coefficients show the magnitude of total (direct plus indirect) effect, and the sign shows whether the effect was positive or negative. Significance levels of the correlations are expressed as n.s. = not significant, * = $P < 0.05$, and ** = $P < 0.001$.

conductivity, and pH of soils across the four commercial fields in 1989 were 0.96 meq/100 g, 10.2 meq/100 g, 1.51 meq/L, 0.94 dS/m, and 6.6, respectively.

Soil moisture at the centers of beds differed among field locations in all 3 yr. In those commercial fields irrigated only in furrows, the soil dried earlier than in those irrigated for part of the season with sprinklers. Although higher levels of soil moisture were maintained for a longer period with sprinkler than with furrow irrigation, there was considerable drying by the end of the season (−0.6 to −4.0 MPa matric potential) under both types of irrigation (12; C. D. McKeen and J. M. Duniway, *unpublished*). Mode of irrigation did not significantly affect disease development.

Soil temperatures were similar at all locations of commercial fields between 20 June and crop maturity for each year. The ranges in daily mean temperatures, followed by ranges in standard deviations in parentheses, were 21.5–25.0 C (1.0–2.0), 23.4–25.2 C (1.2–2.7), and 22.3–27.6 C (1.1–2.0) in 1989, 1990, and 1991, respectively.

DISCUSSION

Populations of *P. parasitica* measured by dilution plating at planting were comparable to populations of *Phytophthora* spp. found in association with perennial crops. For example, propagules of *P. cinnamomi* in soil with Fraser fir roots ranged from 0.05 to 22.84 cfu/g (7,8). Populations of *P. parasitica* on tomato increased during the growing season to levels reported for *P. parasitica* associated with citrus roots (1,4,10). Lutz and Menge (10) demonstrated the influence of irrigation on fluctuations of *P. parasitica* populations and thus the importance of selecting an appropriate time after irrigations for estimating populations. In this study, a precise time of sampling after irrigation events was not possible, but sampling was generally done between 3 and 5 days after an irrigation when the soil was still moist. Increase in populations of *P. parasitica* during the growing season of tomato may have been related to active root growth, such as was demonstrated for *P. parasitica* on citrus (1,10) and postulated for *P. cinnamomi* on Fraser fir (16).

Even though Phytophthora root rot is often considered a "multiple-cycle" disease, there was a positive relationship between initial inoculum and disease development in this study, but it was not as well defined as in a previous study of the same pathosystem in which contrasting inoculum levels were added to soil in fields without a known history of the disease (13). While the previous study showed that the level of inoculum added had significant effects on disease development and yield loss, it was less realistic because inoculum was incorporated into the soil 35 or 45 days after tomatoes were planted. Previous workers have been unable to demonstrate relationships between the severity of root diseases that developed and populations of *Phytophthora* spp. present initially in field soil for *P. capsici* on bell pepper (17), *P. parasitica* var. *nicotianae* on tobacco (22), *Phytophthora* spp. on soybean (21), *P. cinnamomi* on Fraser fir (8), and *P. megasperma* f. sp. *medicaginis* on alfalfa (25). All of the latter studies had rainfall as a common factor, which contrasted with studies on the tomato pathosystem that relied on furrow irrigation for water. Splash dispersal of *Phytophthora* spp. is possible with rainfall but is unlikely with furrow irrigation (2,14), and rates of disease

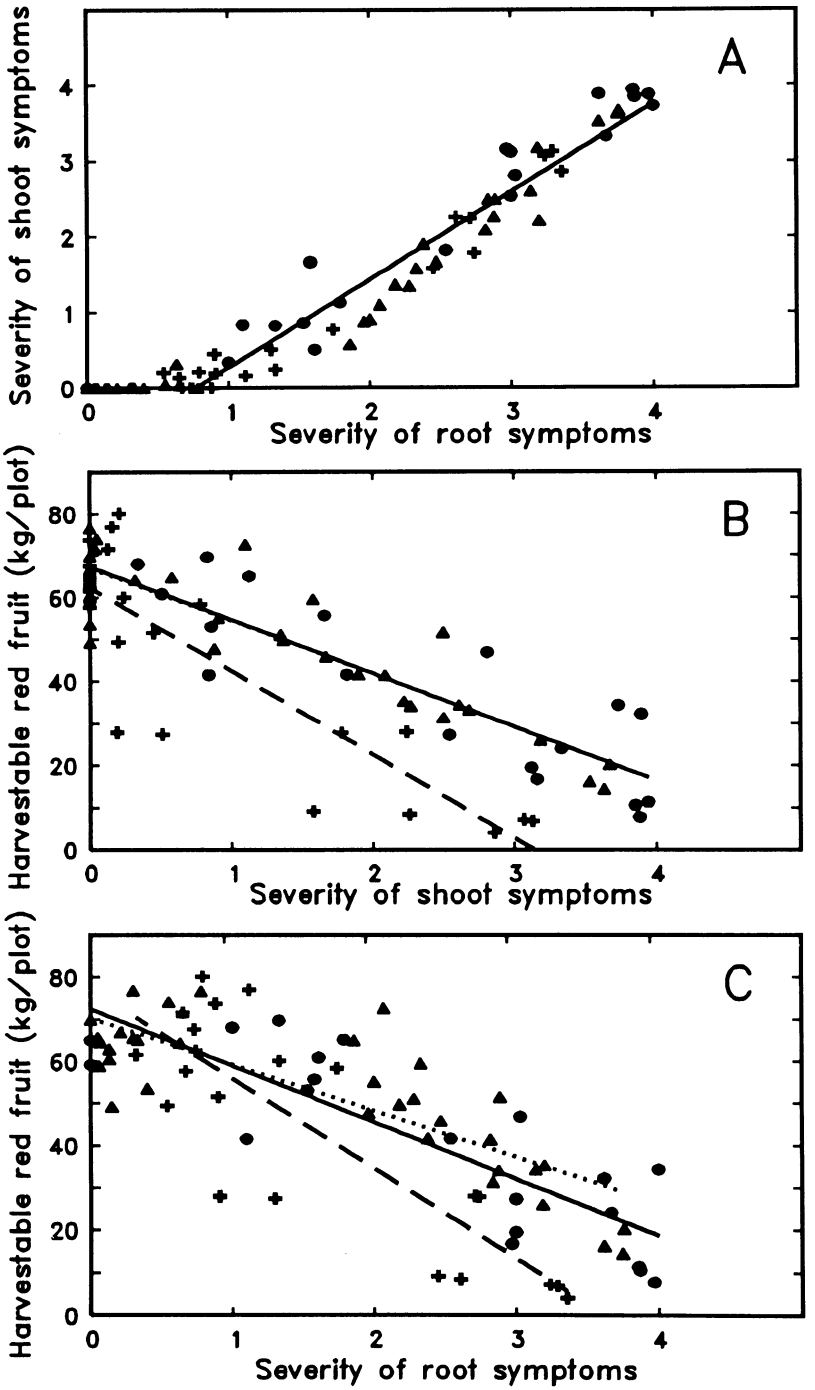

Fig. 2. Relationship of **(A)** final severity of symptoms on shoots to roots, **(B)** fruit yield to final severity of shoot symptoms, and **(C)** fruit yield to final severity of root symptoms. Data represent 11 cultivars of processing tomato in 12 commercial fields during 1989 (●), 1990 (+), and 1991 (▲). A combined regression line is presented for the comparison between shoot and root symptoms because there were no significant differences among years. However, contrasting regression lines are illustrated for the relationships between symptoms and yield when there were significant differences (1989 = solid line, 1990 = dashed line, 1991 = dotted line). Parameter estimates for the regression equations are presented in Table 3. Severities of shoot and root symptoms on each plant were rated on a scale of 0–4, and mean severities and total yields of harvestable red fruit are illustrated for each experimental unit (6-m-long row segment).

development may be very different under rain-fed than furrow-irrigated conditions. Agents that cause splash dispersal may disseminate inoculum to all parts of the plant and plant bed (2), which would not occur with furrow irrigation (14) as the sole source of water for the crop.

Unfortunately, our current methods available for quantification of soilborne populations of *Phytophthora* spp. limit the ability to precisely quantify relationships of inoculum level to disease development and yield loss (12). This became evident when initial populations of *P. parasitica* were detected by dilution plating in about one-half of the plots in which tomatoes developed severe shoot symptoms and yield loss. *P. parasitica* was detected by a baiting assay in all commercial fields before planting. A significant positive correlation between percentage of colonized leaf disks and final disease severity accounted for only 40% of the variation, partly because in some cases the baiting assay reached its upper threshold of detection early in the season (>90% of the leaf disks were colonized in 37% of the experimental units at the time of planting) long before final severities of disease developed. The quantification methods differ greatly in the amount of soil that is assayed, threshold of detection, recovery efficiency above the threshold of detection, and propagule types detected. There is need for a better method of quantification of *P. parasitica* populations in soil, i.e., one that can detect levels as low as those detected by the baiting assay but that also can quantify a wide range of populations in the manner possible with dilution plates at high populations.

The most robust results of this study were the relationships found between root symptoms, shoot symptoms, and yield. These relationships were consistent for 11 commercial cultivars, 12 different commercial fields, and 3 yr. A single linear regression equation described adequately the relationship between shoot and root symptoms for all cultivars, sites, and years (Fig. 2A). This indicated that the relationship between symptom development on aboveground and belowground plant parts was consistent between years and cultivars. Notably, a threshold of root symptoms is required before shoot symptoms are apparent.

The negative linear relationships between final severity of symptoms on both roots and shoots and crop yield (Fig. 2B and C) verify earlier reports on the same system that showed there was no measurable effect of Phytophthora root rot on yield of processing tomatoes until symptoms were visible, and then yield reduction increased with disease severity (13,18). The negative and linear relationships between disease and yield were consistent for 11 cultivars. Evidently, there was little difference among these cultivars in tolerance and/or yield potential under a given level of disease pressure. The slope and intercept of the linear regression line did vary among years, but this difference may be attributed to climate effects on expression of shoot symptoms. A negative linear relationship between disease severity and yield also has been reported for *P. capsici* on pepper (17).

Average soil temperatures were similar across six field locations for specific calendar dates in 1989, 1990, and 1991. Soil temperatures exceeding 30 C early in the season may accelerate epidemic development of Phytophthora root rot on tomato (12), but average daily soil temperatures were below 30 C during the early seasons of 1989 and 1990. In one field in 1991, soil temperatures exceeded 30 C 48–60 days after planting and disease developed rapidly to a final incidence of 81% and mean severity rating of 2.34 (wilting and chlorosis) on shoots. However, it appears that generally other parameters, such as soil texture and pathogen populations, had greater influence on the early phases of epidemic development than did soil temperature. This supports the findings of Agostini et al (1), who suggest that populations of *P. parasitica* associated with citrus roots are related more to active root growth than to soil temperature. We observed no obvious relationship between soil temperature and pathogen populations.

Symptoms of Phytophthora root rot on tomato were more severe in soil with high clay content than in soil with high sand content (Fig. 1). Although the relationships between these interrelated soil properties and development of Phytophthora root rots were anticipated (26), they were not previously quantified for a range of commercial cultivars of an annual host. Although soils of high clay content are likely to have slow rates of internal drainage after irrigation, additional research is needed before disease development can actually be related to features of soil hydrology and water status. Apparently, soil salinity and pH did not affect development of root rot in the field locations in 1989, but these properties did not vary widely. Average exchangeable calcium levels were below those expected to impede zoospore movement (C. D. McKeen and J. M. Duniway, *unpublished*).

In conclusion, these results indicate a positive relationship among populations of *P. parasitica* in soil at planting and disease development in processing tomato. The pattern and nature of such relationships for Phytophthora root rots of tomato and other annual crops have not been precisely defined, partly because methods for pathogen quantification are insufficient. A quantitative method with a low threshold of detection is needed. However, final symptoms of root rot in tomato were more severe in soils with high rates of colonization of leaf disk baits at the time of planting, suggesting that final disease development may be

Table 3. Parameter estimates for linear regression equations using dummy variables[a] comparing the final severity of Phytophthora root rot and harvestable fruit yield during 1989–1991 for 12 commercial field locations and 11 commercial processing tomato cultivars

Variables in regression[b]			Regression	Parameter		Between
Year	Depend.	Indep.	parameter	estimate[c]	SE[d]	years *P*
1989	Shoot	Root	Intercept	−0.803	0.206	
1990	Shoot	Root	Intercept	0.025	0.267	0.0206
1991	Shoot	Root	Intercept	−0.162	0.285	
1989	Shoot	Root	Slope	1.194	0.072	
1990	Shoot	Root	Slope	−0.108	0.109	0.6143
1991	Shoot	Root	Slope	−0.050	0.105	
1989	Yield	Shoot	Intercept	67.445	4.125	
1990	Yield	Shoot	Intercept	−5.040	5.067	0.0002
1991	Yield	Shoot	Intercept	−0.547	4.757	
1989	Yield	Shoot	Slope	−12.749	1.621	
1990	Yield	Shoot	Slope	−7.106	2.593	0.0095
1991	Yield	Shoot	Slope	0.192	2.149	
1989	Yield	Root	Intercept	72.362	5.618	
1990	Yield	Root	Intercept	4.747	7.391	0.0285
1991	Yield	Root	Intercept	−2.137	6.472	
1989	Yield	Root	Slope	−13.416	2.085	
1990	Yield	Root	Slope	−7.835	3.308	0.0044
1991	Yield	Root	Slope	−2.449	2.601	

[a] $R^2 = 0.9418$ for the linear model Shoot $= f$(Root); $R^2 = 0.7140$ for the linear model Yield $= f$(Root); $R^2 = 0.7864$ for the linear model Yield $= f$(Shoot).

[b] Shoot and Root were mean disease severities (0–4) for shoots and roots, respectively, for all plants, and Yield was kilograms of harvestable red fruit, in 6-m-long row segments.

[c] The parameters for 1989 are as shown, but the parameters for 1990 and 1991 must be added to the 1989 parameter to determine the actual value for each year. All parameters were estimated with a single degree of freedom.

[d] Standard error for the parameter estimate; the actual value for each year is shown.

affected by relative amounts of initial inoculum. Final disease severity also increased with early time of epidemic initiation and high soil clay content. There were linear relationships between disease symptoms and yield, suggesting that yield reduction was proportional to severity of symptoms caused by Phytophthora root rot on processing tomato.

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