

## The Role of Salinity in the Development of Phytophthora Root Rot of Citrus

N. S. Blaker and J. D. MacDonald

Former graduate student and associate professor, respectively, Department of Plant Pathology, University of California, Davis 95616.

Present address of first author: Department of Vegetable Crops, University of California, Davis 95616.

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### ABSTRACT

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A field survey of the Coachella Valley, CA, indicated that root rot of citrus, caused by *Phytophthora parasitica*, increased with increasing soil salinity. When rootstock seedlings were grown hydroponically in the greenhouse and exposed briefly to high levels of salinity (EC = 22 dS/m) before inoculation, those of the sweet orange cultivar Pineapple were predisposed to severe root rot, whereas those of the citrange cultivar Troyer were unaffected. However, Troyer seedlings grown for 9 wk in soil salinized to an EC<sub>e</sub> of 3-4 dS/m and infested with *P. parasitica* had 30% of their total

root length decayed by *Phytophthora*, whereas plants in infested nonsaline soil had only 10% decay. Similar results were obtained with Pineapple sweet orange seedlings at even lower levels of soil salinity. Total root growth and production of new roots by Troyer seedlings was greatly inhibited in saline soil. The results suggest that reduced root growth, as well as predisposition, may contribute to the severe root rot observed under saline field conditions.

*Additional key words:* environmental stress, host resistance.

Much of the world's citrus is grown in arid and semiarid regions where irrigation is required for cultivation (9). In these areas, poor quality irrigation water and inadequate soil drainage often result in the accumulation of salts (1,3). Although some cultivars are more tolerant than others, citrus is generally considered a salt-sensitive plant (2,9,12), with growth of most rootstocks adversely affected by salinity levels at which the electrical conductivity of the saturated soil extract (EC<sub>e</sub>) is about 2.5-3.0 decisiemens per meter (dS/m, 1 dS/m = 1 millimho/cm) (3).

Another serious problem in most major citrus-growing areas is *Phytophthora* gummosis and root rot, caused primarily by *Phytophthora parasitica* Dastur and *P. citrophthora* (Smith & Smith) Leonian (8,13,20). Crown infections of susceptible cultivars result in large, expanding cankers that frequently exude copious amounts of amber-colored gum. The root rot phase of the disease, evidenced by decay of small fibrous roots (8,10,13,20), results in general decline and dieback of the leaf canopy. Control of *Phytophthora* gummosis and root rot has focused on water management and use of resistant rootstocks (8,10,20).

In California's Coachella Valley, where soil salinity is a serious problem, *Phytophthora* root rot of citrus was observed to be

unusually severe (J. A. Menge, *personal communication*). Salinity stress can increase *Phytophthora* root rot severity on some plants through increased zoospore attachment on roots (15) and/or inhibition of host defenses (16,21,22). There is some evidence of active host defense responses in avocado roots (11), but the situation with citrus is less clear. Resistance has been attributed partly to rootstock vigor and the capacity to rapidly replace damaged roots (5,10,20). Impaired root vigor was associated with severe *Phytophthora* root rot on citrus seedlings exposed to chronic oxygen stress (20), and salinity stress could impose similar inhibitions. The purpose of this study was to determine the extent to which severity of *Phytophthora* root rot of citrus is influenced by salinity and the possible mechanisms involved.

### MATERIALS AND METHODS

**Field study.** A citrus grove (Cain Ranch, located 35 km south of Coachella, CA) with 10-yr-old mandarin orange (*Citrus reticulata* Blanco 'Fairchild') growing on citrange (*C. sinensis* (L.) Osbeck × *Poncirus trifoliata* (L.) Raf. 'Troyer') rootstock was selected as the study site. The site consisted of two adjoining blocks (hereinafter referred to as Block A and Block B), each with 12 rows of 11 trees. Block A and Block B were approximately 0.25 and 0.35 km, respectively, from the Salton Sea. The soil in both is a Gilman fine sandy loam on an alluvial fan and floodplain with moderate alkalinity and a water table at about 1 m depth (25). The blocks

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were furrow-irrigated at 14- to 21-day intervals throughout the growing season (May–October). The electrical conductivity (EC) of the irrigation water was measured with a YSI model 32 conductance meter (Yellow Springs Instrument Co., Inc., Yellow Springs, OH) (27). *P. parasitica* was detected throughout both blocks by direct isolation from roots on a PVP medium (18) or by baiting from soil samples with citrus leaf disks (24).

In October 1983, soil samples from various depths between 0 and 60 cm were collected with a 2-cm-diameter soil tube from random points throughout the grove 2 days before irrigation and sealed tightly in plastic bags. Gravimetric water contents were determined in the laboratory for each sample to provide a relative comparison between sample locations. Saturated soil extracts were prepared from each sample to measure EC<sub>e</sub> and pH. Tree survival and growth within each block were assessed by tabulating the number of trees replanted or missing during the period from May 1982 to October 1983 and by measuring the trunk diameter 2.5 cm above and below the graft union of 10 randomly selected trees in each block. Leaves were collected from six trees in each block at midday and their water potential ( $\Psi$ ) measured using a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA).

Soil samples containing roots were collected from the top 25 cm of soil, 1 m from the trunks of trees, where fibrous roots were consistently abundant. The golf course turf cutter used to collect the samples had a 25-cm-high  $\times$  10-cm-diameter bucket with four sharply serrated teeth at the cutting edge and a plugger to eject the cores from the bucket. Soil cores were collected 2 days before irrigation in a systematic manner in which every other tree in every other row was sampled in October 1982 and at three monthly intervals during the summer of 1983. At each sampling date, 40–45 soil and root cores were collected and placed in plastic bags. In the laboratory, each core was mixed thoroughly within its plastic bag and a 200-cm<sup>3</sup> subsample removed for EC<sub>e</sub> measurement. The remainder of the core sample was placed on a mesh screen (4.75-mm openings) and the roots recovered by washing away the soil with a fine water spray. A variation of the root intersect method described by Tennant (23) was used to assess the severity of cortical decay in each root sample. Recovered roots were distributed uniformly over a 20.5  $\times$  20.5 cm area against a blue-black cloth and photographed with color slide film. Photographic images of the roots then were projected onto a wall-mounted grid (distance between grid lines = 1.25 cm), and the number of root intersections in 100 vertical and horizontal grid lines was counted to determine total root length and the fraction (expressed as a percentage) of the total showing symptoms of cortical decay. Randomly selected root pieces with cortical decay were cultured on PVP medium to detect *P. parasitica*.

**Greenhouse experiments.** Sweet orange (*C. sinensis* 'Pineapple') and Troyer citrange seedlings were grown from seed in a steam-pasteurized medium of peat and sand (1:1, v/v) in the greenhouse for 14–18 mo before use. The sweet orange rootstock is very susceptible to Phytophthora root rot, while Troyer citrange is reported to have some resistance (13,14). A pathogenic isolate of *P. parasitica* recovered from diseased citrus trees growing in saline soil in Coachella Valley was used in all experiments. Zoospore inoculum was prepared by incubating mycelial disks in soil extract for 24–48 hr to induce sporangium formation (15).

**Solution culture studies.** Seedlings were unpotted and rinsed free of potting medium before placement in 2-L ceramic crocks containing half-strength Hoagland's solution (EC = 1.0 dS/m) (15). The nutrient solutions were aerated continuously and changed every 14 days. Supplemental lighting was provided in the greenhouse to maintain a 14-hr day length. After a 3-wk establishment period, the plants were divided into three treatment groups of eight plants each and salinity stresses imposed. To one group of plants, sufficient NaCl and CaCl<sub>2</sub> (1:10 eq/L) was added to raise the EC of the nutrient solution 2.5 dS/m per day over 8 days to achieve 21 dS/m. A second group of plants was exposed to the same salinity level but in a single application of salts 24 hr before inoculation. The third group of plants was maintained free from salinity stress in half-strength Hoagland's solution. After exposure to the salinity treatments, the solutions in all crocks were

replaced with fresh Hoagland's solution and one-half of the plants in each treatment group were inoculated by adding 10<sup>6</sup> motile zoospores to each crock. Solutions containing inoculum were discarded after 24 hr and replaced with fresh solutions.

Plant roots were harvested 2 wk after inoculation and rinsed with a fine, high-pressure water spray to remove sloughed portions of root cortical tissue. Total root length and decayed root length were estimated as described above, and root pieces from both inoculated and uninoculated plants were cultured on PVP medium to confirm the presence of *P. parasitica*. Experiments were repeated three times with each rootstock and the results analyzed using a two-way analysis of variance. In another experiment, Troyer seedlings were exposed to three consecutive cycles of stress and inoculation, with 2 wk between each treatment cycle. Two weeks after the third and final inoculation, roots were harvested and evaluated as described above. This experiment was repeated twice.

**Root box studies.** To determine how root growth and Phytophthora root rot are affected by chronic exposure to low salinity, citrus seedlings were grown in boxes containing pasteurized river sand. The particle size distribution by weight of the sand was: 2.0–1.0 mm, 45.3%; 1.00–0.50 mm, 27.2%; and 0.50–0.25 mm, 21.3%. The root boxes measured 30  $\times$  22  $\times$  15 cm and were constructed of redwood sides and bottom with an opaque acrylic back. Two holes were drilled in the bottoms for drainage. The front face of the box was a clear glass plate inclined 15° from vertical and covered by opaque acrylic to block light. One seedling was planted in each box, after which the soil profile was saturated and excess water allowed to drain freely. Root boxes then were placed in a growth chamber providing 16 hr of light and temperatures of 25 C day, 21 C night. Seedlings were watered twice a week with 400 ml of tenth-strength Hoagland's solution. This frequency and volume of solution was determined experimentally to be sufficient to wet the soil profile but would quickly equilibrate to matric potential ( $\psi_m$ ) values unfavorable for zoospore release (17). Moisture levels in the boxes were estimated by removing soil samples from depths of 0–9, 9–18, and 18–27 cm before and after irrigation and gravimetrically determining percentage of moisture content. These values were compared with the moisture content of river sand samples drained to  $\psi_m$  values of 0, –10, and –25 millibars (mb) on Büchner funnel tension plates.

One week after the seedlings were transplanted into the root boxes and before any salt or inoculation treatments were imposed, tracings of roots contacting the glass plate were made onto clear acetate sheets with colored felt-tip pens. This process was repeated for each plant at weekly intervals throughout the remainder of the experiments to follow root growth and determine the total number of growing root tips, new roots, and necrotic roots. Ten days after transplanting, the seedlings were divided into two groups of 10 plants each. One group was exposed to salts by adding 50 meq/L of NaCl and CaCl<sub>2</sub> (1:1 eq/L) to the nutrient solution used for irrigation, and the other group was irrigated as before with tenth-strength Hoagland's solution. The EC values of the salinized and unsalinized nutrient solutions were 5.5 and 0.25 dS/m, respectively.

One-half of the plants in each salinity treatment were inoculated with zoospores of *P. parasitica* 3, 5, and 7 wk after establishment in the root boxes. All plants were irrigated with 800 ml of distilled water to fully saturate the sand profile, after which 25 ml of soil extract containing 10<sup>6</sup> motile zoospores was added to plants in the inoculation treatments, followed by another 400 ml of distilled water to help move the zoospores into the root zone. After each inoculation episode, the plants were irrigated as described above, with or without added salt. At the termination of the experiment, the root systems of all plants were recovered and the total root length and percentage of root rot were evaluated as described above. Randomly selected root pieces from all plants also were plated on PVP medium. The effects of salinity on aboveground portions of the plants were evaluated by assessing visual symptoms of Cl<sup>–</sup> toxicity, counting the numbers of remaining leaves and live terminal shoots, and measuring predawn  $\Psi$  with a pressure bomb. Soil samples of 300 cm<sup>3</sup> were removed from each root box for EC<sub>e</sub>

and soil moisture content measurements (27). The entire experiment was repeated twice for each rootstock, and the independent and interactive effects of salinity and *P. parasitica* on total root length and percentage of root rot were evaluated using planned orthogonal comparisons.

## RESULTS

**Field study.** Although trees in both blocks had been planted at the same time, 10 years earlier, a comparison of rootstock and scion diameters showed that those in Block A, closest to the Salton Sea and highest in salinity, were significantly smaller (Table 1). Tree mortality was also higher in Block A, where 22 trees were removed between May 1982 and October 1983, compared with two from Block B. The midday leaf  $\Psi$  among trees in both blocks was similar, with values ranging from  $-17.2$  to  $-12.5$  bars.

The salt and soil moisture levels in Block A were consistently higher than those in Block B during the 1982 and 1983 sampling periods (Table 1). The preirrigation soil moisture in the top 25 cm

TABLE 1. Comparison of soil moisture, salinity level, and tree performance in adjoining blocks of a commercial citrus grove<sup>a</sup>

Parameter	Block A	Block B
Soil moisture <sup>b</sup>	19.2–26.5%	2.6–8.6%
Soil EC <sup>c</sup>	1.0–11.3 dS/m	0.71–3.15 dS/m
Trees removed <sup>d</sup>	22	2
Trunk diameter <sup>e</sup>		
Scion	7.5 ± 1.7 cm	12.1 ± 1.0 cm
Rootstock	9.6 ± 2.6 cm	15.3 ± 1.9 cm

<sup>a</sup>Cain Ranch, Coachella Valley, CA. Blocks A and B approximately 0.25 and 0.35 km from the Salton Sea, respectively.

<sup>b</sup>Preirrigation, October 1983.

<sup>c</sup>Range of 60 samples collected during September 1982.

<sup>d</sup>Of 132, between May 1982 and October 1983.

<sup>e</sup>Means of 10 trees measured in October 1983.

of soil was always highest in Block A and increased with depth because of the high water table. Also, salt concentrations in Block A varied with depth in the soil profile and distance from the Salton Sea. Salt levels were highest at points nearest the Salton Sea and generally decreased with distance. Levels were highest in the top 8 cm of soil (16.2 dS/m) and decreased with depth to 4.4 dS/m at 43 cm. At 60 cm, however, the EC<sub>e</sub> increased to 9.5 dS/m, probably because of the high salt content in the water table. The EC of the irrigation water used in both blocks was 1.09 dS/m in October 1983, and the pH of soil extracts, which ranged from 7.2 to 7.8, did not differ significantly between the blocks.

The mean salinity level in the top 25 cm of soil remained nearly constant (about 3.8 dS/m) in Block A from October 1982 to July 1983 but increased sharply (to 7.1 dS/m) in October 1983. This was attributed to a series of unseasonal heavy rainstorms during August and September 1983 (26) that resulted in large amounts of runoff into the Salton Sea and a rise in the saline water table.

Culturing roots washed from the soil cores collected at each sampling period consistently implicated *P. parasitica* with the symptoms of root decay observed in both blocks. Further, a positive relationship was found between the EC<sub>e</sub> of core samples and the percentage of root length rotted by *P. parasitica* (Fig. 1A–D). The correlation was greatest in the July and October 1983 samplings (Fig. 1C and D, respectively) and was somewhat lower in October 1982 (Fig. 1A). The correlation between percentage of root rot and soil EC<sub>e</sub> was poor for samples taken in May 1983 (Fig. 1B), probably because the samples were taken before the spring flush of root growth (8,19). The May 1983 samples contained few newly formed roots, and the average root length per sample (289 cm) was significantly lower ( $P=0.05$ ) than average root lengths of samples collected in July and October 1983 (475 and 510 cm, respectively). The regression coefficients were tested for homogeneity using Student's *t* test, which showed that the slope of the regression line was significantly greater for July 1983 ( $P=0.01$ ) than for the October samplings (Fig. 1A, C, and D).

**Greenhouse experiments. Solution culture studies.** When

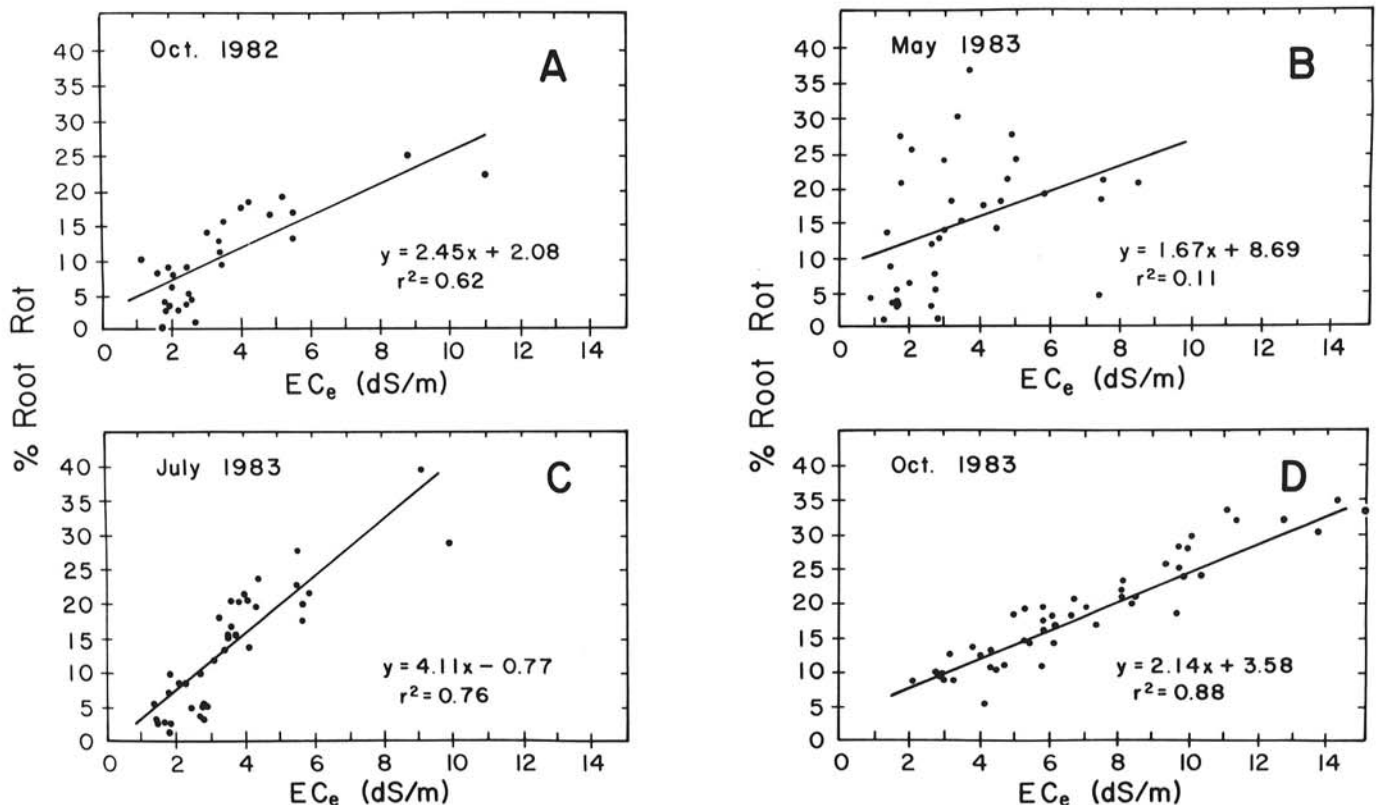
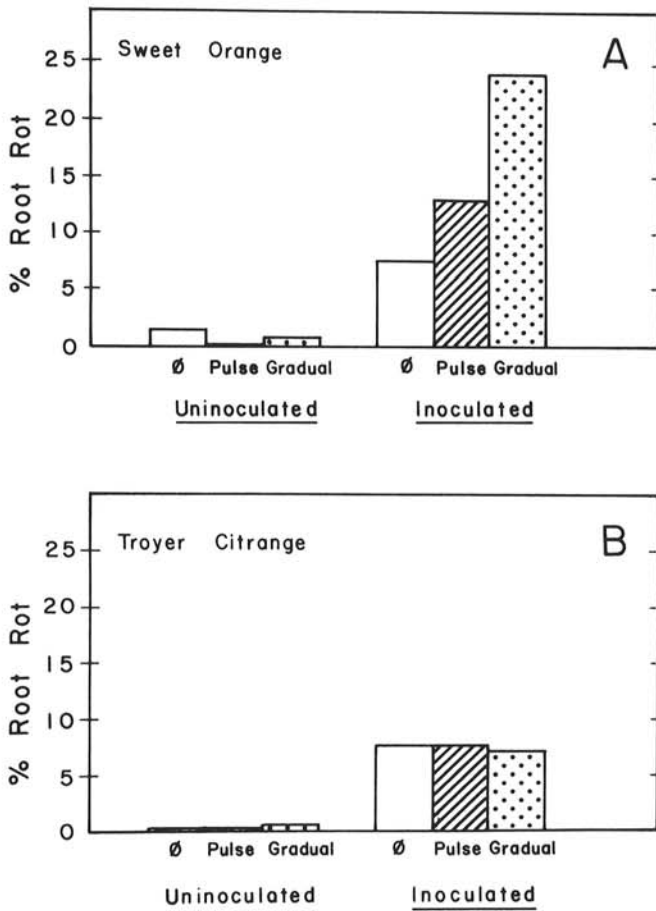


Fig. 1. Relationship between soil salinity and *Phytophthora* root rot of citrus trees grown near the Salton Sea, CA. Soil cores containing roots were collected from the top 25 cm of soil 1 m from the base of trees in A, October 1982, B, May 1983, C, July 1983, and D, October 1983. Each point represents the electrical conductivity of the saturated soil extract (EC<sub>e</sub>, in decisiemens per meter [dS/m]) and percentage of the total root length with cortical decay for each sample.

Pineapple sweet orange seedlings were exposed to high salinity, the severity of subsequent infection by *P. parasitica* greatly increased (Fig. 2A). Plants exposed to salinity either as a single 24-hr pulse treatment or as a gradual increase over several days had 13 and 24% of their root length rotted, respectively, after 2 wk. This compared with 7.4% root rot on nonstressed plants (Fig. 2A). Troyer citrange seedlings, on the other hand, appeared unaffected by the salinity treatments, even when exposed to three consecutive cycles of salt stress and inoculation at 2-wk intervals (Fig. 2B). *P. parasitica* was easily recovered from symptomatic roots in all inoculated treatments but was never recovered from uninoculated plants, and the 1% root decay observed in those treatments (Fig. 2A and B) presumably resulted from natural root death. In the absence of *P. parasitica*, the relatively brief salinity treatments used in these experiments had no effect on total root length or appearance and caused no foliar symptoms.

**Root box studies.** The moisture content of the river sand at 0, -10, and -25 mb  $\psi_m$  was 19.4, 17.1, and 7.3%, respectively. When irrigated with 400 ml of nutrient solution, the moisture content of the sand in the root boxes equilibrated within 15 min to 7.3%. A saturated zone did not develop at the bottom of the root box after irrigations, possibly because the volumes applied were small and any excess water may have been absorbed by the redwood container. The sand in treatments irrigated with saline nutrient solution had an  $EC_e$  of 2.5–4.0 dS/m at harvest.



**Fig. 2.** Percentage of root length rotted in hydroponically grown citrus seedlings exposed to salinity and *Phytophthora parasitica*. Salinity treatments were 0 = no added salt, pulse = EC of nutrient solution increased to 21 dS/m with NaCl and CaCl<sub>2</sub> (1:10) 24 hr before inoculation, and gradual = EC of nutrient solution increased 2.5 dS/m per day over 8 days to a final EC of 21 dS/m before inoculation. **A**, Pineapple sweet orange seedlings received a single salt treatment and inoculation with 10<sup>6</sup> zoospores per plant. **B**, Troyer citrange seedlings received three consecutive treatments of salt and inoculation at 2-wk intervals. Data are from a representative experiment and are the means of four plants per treatment. LSD = 4.9% for **A** and 1.8% for **B** at  $P = 0.05$ .

Both salinity and *P. parasitica* had significant effects on total root length of plants over the 10-wk experiments (Table 2). Inoculation reduced Troyer citrange root length to about 50% of that of the controls, whereas salinity (2.5–4.0 dS/m) caused a 75% reduction ( $P = 0.01$ ). Pineapple sweet orange seedlings appeared very sensitive to salinity, as all plants exposed to soil  $EC_e$  values of 3.0–4.0 dS/m died after 5 wk. Experiments were repeated using lower levels of salinity (1.2–2.0 dS/m) and all plants survived through harvest, at which time *P. parasitica* and salinity were found to cause 40 and 45% reductions in root length, respectively (Table 2,  $P = 0.05$ ). Inoculation with *P. parasitica* significantly ( $P = 0.01$ ) affected the percentage of root length rotted in both citrus species (Table 2), and the interaction between salinity and *P. parasitica* also was significant ( $P = 0.01$  for Troyer,  $P = 0.05$  for sweet orange). Uninoculated seedlings of both cultivars had  $\leq 1.2\%$  cortical decay, which occurred in the absence of any detectable pathogen.

The number of elongating roots increased and then declined in all treatments, but the decline was most pronounced in plants exposed to salinity (Fig. 3). Seedlings in nonsaline sand averaged

**TABLE 2.** Effect of soil salinity and *Phytophthora parasitica* on total root length and root rot severity at harvest in citrus seedlings grown in root boxes

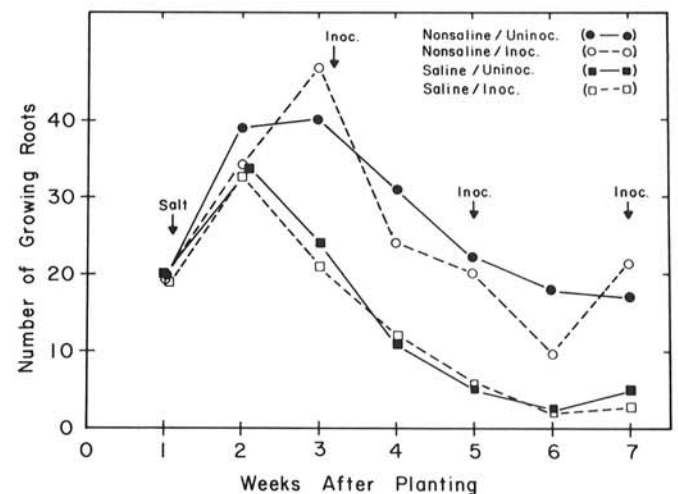
Rootstock	Treatment <sup>a</sup>		Soil $EC_e^b$ (dS/m)	Root length <sup>c</sup> (cm)	Root rot <sup>d</sup> (%)
	Salt	Inoculation			
Troyer citrange	–	–	0.74–1.02	1,926	0.4
	–	+	0.35–0.71	952	9.9
	+	–	2.98–4.03	477	0.2
	+	+	2.51–3.40	474	30.4
Pineapple sweet orange	–	–	0.29–0.71	232	0.2
	–	+	0.23–0.57	140	12.4
	+	–	1.55–2.01	152	1.2
	+	+	1.20–1.98	110	20.8

<sup>a</sup> + = Exposure of plants to salt or inoculation treatments, – = untreated controls.

<sup>b</sup> Electrical conductivity of saturated soil extract in decisiemens per meter; ranges from five replicate treatments.

<sup>c</sup> Means of five replicates. Significantly affected by both inoculation and salt ( $P = 0.01$  and 0.05 for Troyer citrange and Pineapple sweet orange, respectively).

<sup>d</sup> Percentage of total root length with cortical decay symptoms; means of five replicates. Significantly affected by inoculation ( $P = 0.01$  for both species) and interaction of salt and inoculation ( $P = 0.01$  and 0.05 for Troyer citrange and Pineapple sweet orange, respectively).



**Fig. 3.** Root growth of Troyer citrange seedlings in nonsaline and saline sand. Plants were inoculated with 10<sup>6</sup> zoospores of *Phytophthora parasitica* per plant 3, 5, and 7 wk after planting. Root growth was monitored at weekly intervals and is expressed as the number of elongating root tips per plant, based on the mean of five replicates.

over 40 growing root tips in contact with the glass face of the root box 3–4 wk after planting, whereas those in saline soil averaged less than 25. In addition to smaller numbers of growing roots, salinity reduced the number of new roots produced each week by the Troyer citrange seedlings (Fig. 4). Plants growing in nonsaline soil produced new roots continuously and had nearly 100 new roots per plant in contact with the glass face of the root box after 8 wk. Plants grown in saline sand for 8 wk, however, had an average of only 50 new roots per plant visible on the glass window (Fig. 4). In contrast to salinity, *P. parasitica* had no impact on production and growth of roots (Figs. 3 and 4). Attempts to measure root growth and formation in Pineapple sweet orange were unsuccessful because the root systems were much smaller than those of Troyer (Table 2) and few roots (approximately four new or growing roots per plant per week) intersected the glass face of the root box.

Both inoculated and uninoculated Troyer citrange plants grown for 10 wk in saline sand showed symptoms of chlorosis and bronzing typical of  $Cl^-$  toxicity (1). In contrast to Troyer, Pineapple sweet orange seedlings became chlorotic and shed their leaves after 8 wk at relatively low salinities ( $EC_e$  1.5–2.2 dS/m) and seven had dead terminal buds. Troyer plants in saline soil had average predawn leaf  $\Psi$  values of  $-7.5$  bars, whereas those in nonsaline soil had  $\Psi$  values of  $-3.5$  bars. Extensive leaf drop by Pineapple sweet orange seedlings made  $\Psi$  measurements impossible.

## DISCUSSION

The results of our field and greenhouse experiments show that a strong relationship exists between the level of soil salinity and the severity of Phytophthora root rot of citrus. In the Coachella Valley citrus grove, a positive correlation ( $r^2 = 0.62-0.88$ ) was found between salinity level and Phytophthora root rot severity on Troyer citrange rootstock during the October 1982, July 1983, and October 1983 sample periods (Fig. 1). The overall higher levels of root rot in the July 1983 samplings than in the two October samplings may reflect differences in pathogen populations, which peak with the higher soil temperatures of July–September and decline as soil temperatures drop in October (8). Similarly, the poor correlation between root rot and salinity in May 1983 (Fig. 1B) probably resulted from seasonal variation in root growth as well as pathogen activity.

We should point out that salinity was not the only variable that could have influenced disease severity at the field site. A gradient in soil moisture extended across the blocks, and the most saline areas also had the highest preirrigation moisture levels (Table 1). Such a

relationship between soil moisture and salinity is common in salt-affected soils (1) and makes assessment of the independent effects of salinity in the field difficult. Our greenhouse studies minimized differences in soil moisture, however, and root rot severity clearly was related to salinity treatments (Table 2), suggesting salinity was a major factor influencing disease severity in the field.

Phytophthora root rot severity in citrus could be influenced by high salinity in several ways. The isolate of *P. parasitica* we recovered from the Coachella Valley appeared to be stimulated by salinity, forming maximum numbers of sporangia at  $EC_e$  values of 5–37 dS/m (4). While this could have led to somewhat higher inoculum levels in some parts of our field site, it probably was not an important factor in the root box experiments, where  $EC_e$  values ranged between 2.5 and 4.0 dS/m. Furthermore, measurements of soil moisture in the root boxes indicated that within 15 min of irrigation, the moisture content of the sand equilibrated to  $\leq 7.3\%$  ( $\psi_m \leq -25$  mb), which would have greatly restricted zoospore release (17). Thus, in the controlled experiments, activity by *P. parasitica* probably did not differ greatly between treatments.

Although pathogen activity in the root box experiments was probably very similar in the low- and high-salinity treatments, root initiation and growth differed greatly. Measurements of Troyer citrange seedlings revealed sharp declines in root development in saline vs. nonsaline treatments (Figs. 3 and 4), resulting in a significant reduction in total root length at harvest (Table 2). The ability of citrus to continually produce new roots (Fig. 4), replacing those rotted by *P. parasitica*, indicates why only a small percentage of the total root system may show symptoms of decay at any given time. Indeed, root regeneration has been suggested as an important factor in the field resistance of some rootstocks to Phytophthora root rot (5,11). Salinity stress inhibits root initiation and growth (Figs. 3 and 4) so that, over time, a greater percentage of the total root system would tend to be diseased roots. In this respect, the results resemble those of Stolzy et al (20), who showed that increased root rot severity in poorly aerated soils was due, at least in part, to impaired root regeneration.

Root regeneration, however, does not appear to be the only factor involved in the resistance of Troyer to Phytophthora root rot. When Troyer and Pineapple orange seedlings were grown in nonsaline nutrient solution, relatively low levels of root rot developed after inoculation with *P. parasitica* (Fig. 2A and B). After a one-time brief preinoculation exposure to high salinity ( $EC = 22$  dS/m), Pineapple sweet orange seedlings were predisposed to severe root rot in a manner resembling that reported for chrysanthemum and tomato (15,16,21), but no such change in susceptibility was induced in Troyer citrange—even with repeated exposures to salt stress and inoculum (Fig. 2B). Because these were relatively short-term experiments with only brief episodes of stress, the differences in root rot severity between the two rootstocks cannot be attributed just to differences in root vigor. In other plants, salinity stress significantly increases root rot severity through increased zoospore attachment on roots (15) and dysfunction of host defense mechanisms (16,21,22). Whereas salinity stress can predispose Pineapple sweet orange to severe root rot, the mechanisms that serve to limit root infections in Troyer clearly were not compromised by these salinity treatments.

Troyer citrange may be better able than Pineapple sweet orange to tolerate brief periods of salinity stress. Differences in the sensitivity of citrus rootstocks to salinity and  $Cl^-$  have been reported (6,7). The reports indicate, however, that trees grown on sweet orange rootstock are more tolerant of salinity than those grown on Troyer citrange (7). Although Pineapple sweet orange appeared much more sensitive to chronic salinity than Troyer citrange in our root box experiments, these were not grafted plants, and ion accumulation and toxicity in citrus are influenced by both the rootstock and the scion. Thus, our observations of foliar injury and relative sensitivity may not accurately reflect the performance of grafted trees in field soils.

The results presented here clearly show that Phytophthora root rot of citrus is more severe in the presence of salinity. Increased disease could result from increased tissue susceptibility and/or inhibition of root growth and regeneration. These effects,

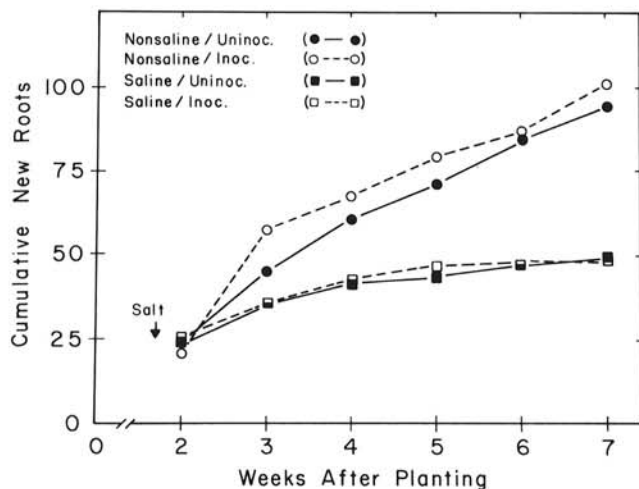


Fig. 4. Formation of new roots by Troyer citrange seedlings grown in saline and nonsaline sand. Plants were inoculated with 10 zoospores of *Phytophthora parasitica* per plant 3, 5, and 7 wk after planting. The numbers of new roots are based on the mean of five replicate plants per treatment.

combined with the ability of *P. parasitica* to tolerate high levels of salinity (4), could significantly diminish the effectiveness of *Phytophthora*-resistant rootstocks in salt-affected soils.

#### LITERATURE CITED

1. Backlund, V. L., and Hoppes, R. R. 1984. Status of soil salinity in California. *Calif. Agric.* 38(10):8-9.
2. Bernstein, L. 1969. Salinity factors and their limits for citrus culture. *Proc. Int. Citrus Symp. Ist.* 3:1779-1782.
3. Bernstein, L. 1975. Effects of salinity and sodicity on plant growth. *Annu. Rev. Phytopathol.* 13:295-312.
4. Blaker, N. S., and MacDonald, J. D. 1985. Effect of soil salinity on the formation of sporangia and zoospores by three isolates of *Phytophthora*. *Phytopathology* 75:270-274.
5. Broadbent, P., Fraser, L. R., and Waterworth, Y. 1971. The reaction of seedlings of *Citrus* spp. and related genera to *Phytophthora citrophthora*. *Proc. Linn. Soc. N.S.W.* 96:119-127.
6. Cooper, W. C., Gorton, B. S., and Olson, E. O. 1952. Ionic accumulation in citrus as influenced by rootstock and scion and concentration of salt and boron in the substrate. *Plant Physiol.* 27:191-203.
7. Cooper, W. C., and Shull, A. V. 1953. Salt tolerance of and accumulation of sodium and chloride ions in grapefruit on various rootstocks grown in naturally saline soil. *Proc. Rio Grande Val. Hortic. Inst.* 7:107-117.
8. Feld, S. 1982. Studies on the role of irrigation and soil water matric potential on *Phytophthora parasitica* root rot disease of citrus. Ph.D. thesis. University of California, Riverside. 107 pp.
9. Furr, J. R., and Ream, C. L. 1969. Breeding citrus rootstocks for salt tolerance. *Proc. Int. Citrus Symp. Ist.* 1:373-380.
10. Grimm, G. R., and Hutchison, D. J. 1973. A procedure for evaluating resistance of citrus seedlings to *Phytophthora parasitica*. *Plant Dis. Rep.* 57:669-672.
11. Kellman, M. K., and Coffey, M. D. 1985. Quantitative comparison of the resistance to *Phytophthora* root rot in three avocado rootstocks. *Phytopathology* 75:230-234.
12. Kirkpatrick, J. D., and Bitters, W. P. 1969. Physiological and morphological response of various citrus rootstocks to salinity. *Proc. Int. Citrus Symp. Ist.* 1:391-399.
13. Klotz, L. J. 1978. Fungal, bacterial and nonparasitic diseases and injuries originating in the seedbed, nursery and orchard. Pages 1-66 in: *The Citrus Industry. Vol. 4. Crop Protection.* W. Reuther, E. C. Calavan, and G. F. Carman, eds. Agricultural Sciences Publications, University of California, Richmond. 326 pp.
14. Klotz, L. J., Bitters, W. P., DeWolfe, T. A., and Garber, M. J. 1968. Some factors in resistance of citrus to *Phytophthora* spp. *Plant Dis. Rep.* 52:952-955.
15. MacDonald, J. D. 1982. Effect of salinity stress on the development of *Phytophthora* root rot of chrysanthemum. *Phytopathology* 72:214-219.
16. MacDonald, J. D. 1984. Salinity effects on the susceptibility of chrysanthemum roots to *Phytophthora cryptogea*. *Phytopathology* 74:621-624.
17. MacDonald, J. D., and Duniway, J. M. 1978. Influence of the matric and osmotic components of water potential on zoospore discharge in *Phytophthora*. *Phytopathology* 68:751-757.
18. Mircetich, S. M., and Matheron, M. E. 1976. *Phytophthora* root and crown rot of cherry trees. *Phytopathology* 66:549-558.
19. Reed, H. S., and MacDougal, D. T. 1937. Periodicity in the growth of the orange tree. *Growth* 1:371-373.
20. Stolzy, L. H., Letey, J., Klotz, L., and Lubanauskas, C. K. 1965. Water and aeration as factors in root decay of *Citrus siensis*. *Phytopathology* 55:270-275.
21. Swiecki, T. J. 1984. Interactions between salinity and *Phytophthora* root rots of chrysanthemum and tomato. Ph.D. thesis. University of California, Davis. 109 pp.
22. Swiecki, T. J., and MacDonald, J. D. 1982. Histopathology of chrysanthemum roots exposed to salinity and *Phytophthora cryptogea*. (Abstr.) *Phytopathology* 72:995.
23. Tennant, D. 1975. A test of a modified line intersect method of estimating root length. *J. Ecol.* 63:995-1001.
24. Thompson, S. V., and Allen, R. M. 1976. Mechanisms of survival of zoospores of *Phytophthora parasitica* in irrigation water. *Phytopathology* 66:1198-1202.
25. U.S. Department of Agriculture. 1980. Soil survey of Riverside County, California, Coachella Valley Area. Soil Conservation Service in Cooperation with University of California Agricultural Experiment Station. 89 pp.
26. U.S. Environmental Data and Information Service, National Oceanic and Atmospheric Administration. 1983. Climatological Data, California. 87:6-10.
27. U.S. Salinity Laboratory. 1954. Diagnosis and improvement of saline and alkali soils. U.S. Dep. Agric. Handb. 60. 160 pp.