Effect of Soil pH on Susceptibility of Peach to Pseudomonas syringae

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ABSTRACT

'Elberta' peach seedlings were grown in pots of soil from a peach orchard where bacterial canker had occurred, and were artifically inoculated with *Pseudomonas syringae* after they had become dormant. Seven weeks later, three of five of the inoculated trees in unadjusted soil (pH 5.6) had died. Two of five plants in soil adjusted to pH 6.1 with $MgCO_3$ also died, but no plants died in soil adjusted to pH 6.4, 6.6, 6.9, or 7.2 with $CaCO_3$ or $MgCO_3$. No differences in stem length, fresh weight of roots, or discoloration of feeder roots were observed among the treatments. However, percentage of dry matter in roots was greater for plants grown at pH 6.4-6.9 than at 5.6, 6.1, or 7.2. Vesicular-arbuscular mycorrhizae were present in 77 to 94% of the feeder roots, with fewest roots infected at pH 6.6 where $MgCO_3$ was used. Numbers of propagules of *Pythium* spp. in soil, and recovery from roots were positively correlated with soil pH. In December, populations of *Criconemoides xenoplax* was greater in soil adjusted above pH 6.1, but differences were not significant in March and April.

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The bacterial canker disease of peach (*Prunus persica* L. Batsch) trees caused by *Pseudomonas syringae* Van Hall is associated with the loss of peach trees in the central valley of California (11) and the southeastern United States (9, 23). The disease occurs on the aboveground parts of the trees, and may result in localized cankers or death of entire limbs or trees (11, 23). Virulent strains of *P. syringae*, however, have been readily isolated from trunks and twigs of peach trees in commercial orchards in Georgia and South Carolina, where little or no damage from bacterial canker was observed (10). Along with other evidence (5, 10, 21, 28), this isolation suggests that peach trees may be predisposed to infection by the bacterial canker organism before trees are damaged.

High populations of *Criconemoides xenoplax* Raski are usually associated with peach trees injured by bacterial canker (6, 11, 17, 28). Fumigation of soil with nematicides reduces susceptibility of trees to *P. syringae* (6, 12, 15). Further, *C. xenoplax* and species of *Pythium* have been shown experimentally to predispose peach trees to bacterial canker (21). However, in the southeast, peach trees parasitized by *C. xenoplax* are not always diseased from bacterial canker, even though *P. syringae* may be present (28). Thus, other factors present in the soil may also affect the susceptibility of peach trees to the bacterial canker organism.

One possible factor is soil pH. The soil pH in peach orchards in the southeast generally ranges from 4.5 to 5.5 but it may be as low as 4.0 in some areas. Lime is usually applied to the soil before peaches are planted, and this practice has been observed to reduce the occurrence of bacterial canker (N. E. McGlohon, *personal communication*). However, no data are available to indicate which soil pH might be most favorable for the survival of peach trees on old peach land where bacterial canker has occurred. This paper reports on the effects of soil pH on root growth, soil and root microflora, nematodes, and susceptibility to *P. syringae* of peach seedlings grown in pots with soil from an old peach orchard site.

MATERIALS AND METHODS.—In June 1973, soil was collected 7.5 to 30 cm deep around peach trees recently killed by bacterial canker in an old orchard site (28). The soil was passed through a soil shredder fitted with a 1.25-cm screen. We removed 10 samples of soil and determined the pH to be 5.6, after mixing 50 cm^3 of soil with 100 ml of 0.01 M calcium chloride (26) and reading it with a Beckman Zeromatic II pH meter. Also, the soil was assayed for nematodes. Samples were treated with Electrasol (29), and nematodes were extracted by the sugar centrifugation process (19). Nematodes were identified and counted under a stereoscopic microscope at × 25.

After a previously determined amount of powdered $CaCO_3$ or $MgCO_3$ (Fisher) had been added to give the desired pH, enough soil to fill 10 clay pots, 20 cm in diameter was mixed in a cement mixer for 10 minutes. Samples were removed from each treatment, and the pH was determined as before. Amounts of $CaCO_3$ or $MgCO_3$ added per liter of soil and resulting pH levels were as follows: 1.39 g $CaCO_3$, pH 6.4; 3.0 g $CaCO_3$, pH 6.9; 5.0 g $CaCO_3$, pH 7.2; 0.6 g $MgCO_3$, pH 6.1; 1.21 g $MgCO_3$, pH 6.4; 1.6 g $MgCO_3$, pH 6.6. Controls comprised nonamended soil with unadjusted pH in separate groups of pots. One group of controls was mixed in the cement mixer, but the other group was not, because the soil formed tiny beads during the mixing and changed in texture.

Five-week-old Elberta peach seedlings approximately 25 cm tall, grown in 7-cm diameter peat pots, were transplanted into each pot of soil. These were grown in the greenhouse (23-30 C) for 10 weeks and fertilized

biweekly with a complete liquid fertilizer (12-6-6). The plants were then arranged randomly in a lathhouse, with the pots sunk in a bed of wood shavings to prevent large soil temperature fluctuations. The soil was kept moist, but not fertilized again.

Pseudomonas syringae, obtained from peach in South Carolina, was kept in sterile water at 4 C (7). An aqueous suspension with approximately 4.2×10^8 cells per ml was prepared from cultures grown on nutrient agar for 24 hours. Five of the 10 plants in each treatment were inoculated with *P. syringae* on 19 December 1973, when the plants were dormant. With a sterilized 0.31-cm (1/8-inch) drill, we made a hole through the stem bark and slightly into its xylem, 10 cm above the soil line; 0.05 ml of inoculum was deposited into each hole with a pipet. The remaining five plants in each treatment were similarly drilled, but not inoculated.

Eleven weeks after inoculation, the five uninoculated plants in each treatment were harvested. Each plant stem was examined for browning in the bark and wood. The soil was shaken from the roots and collected in a polyethylene bag. Root systems were washed free of soil with tap water and immediately examined macroscopically, and the percentage of discolored feeder roots was estimated for each plant. Samples of roots were placed in 500-cc Erlenmeyer flasks containing sterile distilled water and shaken for 1 hour, to remove the remaining soil particles. The remaining roots were dried in an oven at 80 C for 48 hours and weighed.

We surface-sterilized rootlets 1.5- 2.0 cm long by dipping them in 70% ethyl alcohol and drying them on sterile paper towels (22). Sixteen rootlets per plant were plated on a medium selective for *Pythium* spp. (27), and 16 similar rootlets were placed on acidified potato-dextrose agar (PDA).

We examined feeder roots for the presence of endomycorrhizae, using the root-clearing and staining technique described by Bird et al. (2). To determine the degree of infestation, a 1-cm terminal portion of each of 25 feeder roots per plant was examined under a microscope at × 80. Then the percentage of root with vesicular-arbuscular (VA) mycorrhizae was estimated (D. H. Marx, *personal communication*).

The soil from each pot was passed through 4.6-mm screen, and 10 g was removed and dried, to determine the percentage of moisture. A 50-cc sample was also removed, and the soil pH was determined. The population of *Pythium* spp. in soil was determined by use of the technique and selective medium developed by Mircetich (22). Populations of other fungi, bacteria, and actinomycetes were also estimated. Soil (10 g) was suspended in 100 ml of sterile water, and a dilution series was prepared. To estimate the total number of propagules, we spread 0.2 ml of soil suspension on acidified PDA for fungi and used a weak peptone-dextrose agar (14) to determine populations of bacteria and actinomycetes.

Populations of nematodes in 150 cm^3 soil samples from each pot were determined as described previously.

All data were subjected to an analysis of variance, and

TABLE 1. Susceptibility to *Pseudomonas syringae* of peach seedlings grown in pots with peach-orchard soil adjusted to various pH levels

Treatment[a]	Inoculated with *P. syringae*[b]	Fraction with stem canker[c]	Reisolation of *P. syringae* from diseased plants[d] (%)
Control, unmixed (pH 5.6)	+	3/5	66
	−	1/5	100
Control, mixed (pH 5.6)	+	3/5	100
	−	2/5	0
$MgCO_3$ (pH 6.1)	+	2/5	100
	−	0/5	0
$MgCO_3$ (pH 6.4)	+	0/5	0
	−	0/5	0
$MgCO_3$ (pH 6.6)	+	0/5	0
	−	0/5	0
$CaCO_3$ (pH 6.4)	+	0/5	0
	−	0/5	0
$CaCO_3$ (pH 6.9)	+	0/5	0
	−	0/5	0
$CaCO_3$ (pH 7.2)	+	0/5	0
	−	0/5	0

[a]Soil adjusted to various pH levels by amending with $CaCO_3$ or $MgCO_3$ and mixing in a cement mixer. Controls were in unadjusted soil used before (unmixed) or after (mixed) mixing.

[b]Five dormant plants in each treatment were inoculated with *P. syringae* suspended in sterile distilled water (+) or left uninoculated (−) 6 months after seedlings were transplanted.

[c]Number of seedlings with stem canker per number of seedlings inoculated.

[d]*P. syringae* was reisolated only from diseased plants.

Duncan's multiple range test was used, when appropriate.

RESULTS.—Approximately 7 weeks after inoculation, peach seedlings grown only in soil at pH 5.6 or 6.1 developed stem cankers resembling those of naturally infected peach orchard trees (Table 1). Stem bark of diseased seedlings appeared brown and water-soaked down to, but not below, the soil level. A characteristic sour sap odor was evident when the bark was cut. Entire stems were usually affected, and no localized cankers were observed.

Although the plants were inoculated on 19 December when about 41% of the chilling requirements was satisfied, disease symptoms were not observed until 8 February when the plants had received 66% of the chilling necessary to break dormancy. The appearance of disease symptoms was preceded by 23 days with average daily maximum and minimum temperatures of 20 C (68 F) and 11.1 C (52 F), respectively, and a drop to a minimum of −1.1 C (30 F) on 5 February. No additional plants became diseased after 8 February, even though the temperature dropped below freezing again on 25 February.

Of the plants inoculated with *P. syringae*, three of five were diseased in the pH5.6 soil treatment, and two of five were diseased in the pH 6.1 soil treatment. However, of the uninoculated plants, one of five in the unmixed and two of five in the mixed control (pH 5.6) soil were also diseased. No plants either inoculated or uninoculated, grown at pH 6.4 or above became diseased. We tried to isolate *P. syringae* from each plant by cutting off the upper 30 cm of stem and using the isolation technique of Dowler and Weaver (10). The stems ranged from 67 to 85 cm in height and averaged 79 cm, but the averages of treatment groups did not differ significantly. The bacterium was recovered from all but one of the diseased

TABLE 2. Effect of soil pH on percentage of dry matter, abundance of mycorrhizae, and occurrence of fungi from peach seedling roots

Treatment	Dry matter (%)	Feeder roots with vesicular-arbuscular mycorrhizae (%)	Rootlets from which fungi were recovered (%)[x]		Diseased plants (%)
			Pythium spp.	*Fusarium* spp.	
Control, unmixed (pH 5.6)	38.7 b[y]	88.1 a	1.2 b	48.7 bc	60
Control, mixed (pH 5.6)	40.0 b	92.6 a	1.2 b	36.2 bc	60
$MgCO_3$ (pH 6.1)	39.0 b	94.0 a	1.2 b	51.2 abc	40
$MgCO_3$ (pH 6.4)	46.1 a	88.4 a	3.7 b	56.2 ab	0
$MgCO_3$ (pH 6.6)	45.7 a	77.6 b	10.0 b	37.5 c	0
$CaCO_3$ (pH 6.4)	40.0 b	93.3 a	6.2 b	45.0 abc	0
$CaCO_3$ (pH 6.9)	44.5 a	91.4 a	16.2 ab	60.0 ab	0
$CaCO_3$ (pH 7.2)	42.9 ab	90.6 a	33.7 a	62.5 a	0
r value [z]	+0.43**	−0.06 NS	+0.51***	*0.16 NS	

[x]Sixteen rootlet segments 1.5 to 2.0 cm long were plated for each of five plants per treatment.
[y]Numbers followed by different letters differ significantly, $P = 0.05$ by Duncan's multiple range test.
[z]Coefficient of correlation (r) with soil pH. Level of significance: * indicates P=0.05; ** indicates P=0.01; *** indicates P=0.001; NS indicates no significance.

TABLE 3. Effects of propagule populations of fungi and bacteria in pots with peach orchard soil adjusted to various pH levels with $CaCO_3$ and $MgCO_3$ on disease development in peach seedlings

Treatment	Propagules per/g (dry wt) of soil[w] (av)			Diseased plants (%)
	Pythium spp.	Total fungi ($\times 10^3$)	Bacteria and actinomycetes ($\times 10^5$)[x]	
Control, unmixed (pH 5.6)	20.8 e[y]	40.6	75.1	60
Control, mixed (pH 5.6)	24.0 e	55.1	98.8	60
$MgCO_3$ (pH 6.1)	116.8 d	46.7	56.2	40
$MgCO_3$ (pH 6.4)	165.1 cd	57.4	45.6	0
$MgCO_3$ (pH 6.6)	227.8 bc	47.6	56.5	0
$CaCO_3$ (pH 6.4)	162.9 cd	47.3	42.8	0
$CaCO_3$ (pH 6.9)	368.9 a	47.5	42.4	0
$CaCO_3$ (pH 7.2)	266.4 ab	54.6	45.4	0
r value[z]	+0.84***	+0.26*	−0.36*	

[w]Data are averages of five samples per treatment. Samples were removed from soil 8 months after treatment.
[x]No significant difference.
[y]Numbers followed by different letters differ significantly, P=0.05, by Duncan's multiple range test.
[z]Coefficient of correlation (r) with soil pH. Level of significance: * indicates P=0.05; ** indicates P=0.01; *** indicates P=0.001.

TABLE 4. Numbers of *Criconemoides xenoplax* around roots of peach seedlings grown in pots of peach orchard soil adjusted to various pH levels

Treatment	Nematode counts (no./150 cc soil)				Diseased plants (%)
	Uninoculated seedlings, sampled:		Seedlings inoculated with *Pseudomonas syringae*[y] and sampled:		
	28 Dec 73	14 Mar 74	28 Dec 73	15 Apr 74	
Control, unmixed (pH 5.6)	780 bc[z]	1,228 a	789 cd	970 a	60
Control, mixed (pH 5.6)	552 c	964 a	483 d	1,054 a	60
$MgCO_3$ (pH 6.1)	978 abc	842 a	1,032 bcd	1,128 a	40
$MgCO_3$ (pH 6.4)	1,209 ab	1,244 a	1,635 ab	916 a	0
$MgCO_3$ (pH 6.6)	1,599 a	2,340 a	1,728 ab	900 a	0
$CaCO_3$ (pH 6.4)	1,320 a	1,040 a	1,488 abc	1,252 a	0
$CaCO_3$ (pH 6.9)	1,518 a	1,476 a	1,753 a	1,740 a	0
$CaCO_3$ (pH 7.2)	1,701 a	1,296 a	2,301 a	1,310 a	0

[y]Plants were inoculated on 19 Dec 1973.

[z]Numbers followed by different letters differ significantly, $P = 0.05$ by Duncan's multiple range test. Data represent average numbers of nematodes per 150 cc of soil in five pots per treatment.

plants that had been inoculated with *P. syringae*, but it was also isolated from one of the three diseased uninoculated plants (Table 1). The plants which had been inoculated with *P. syringae*, but which remained symptomless, leafed out by mid-April, whereas many diseased plants that had completely dead stems by this time developed sucker shoots from below-ground parts. Soil from each pot was assayed for nematodes at this time, and the plants were discarded.

A second experiment was similarly conducted in 1974-75. Peach seedlings were grown in pots of soil with a pH of 4.6 and in soil adjusted to pH 6.5 by amending with $CaCO_3$. Fifteen plants in each treatment were inoculated with *P. syringae* on 9 December and five were left uninoculated. Disease symptoms were first observed on 24 January when the plants had received approximately 87% of the chilling required to break dormancy. Six of 15 inoculated plants grown at pH 4.6 were killed. No uninoculated plants and only one inoculated plant grown at pH 6.5 were diseased. *Pseudomonas syringae* was reisolated from all diseased plants.

Examination of the root systems of uninoculated plants from the first experiment revealed that 90-100% of the feeder roots were brown in all treatments. The root systems were well developed, and treatments did not differ in fresh weight of the roots. However, roots grown in soil raised to pH 6.4 and 6.6 with $MgCO_3$ or pH 6.9 with $CaCO_3$ had a significantly greater percentage of dry matter than roots in other treatments (Table 2).

Vesicular-arbuscular (VA) mycorrhizae were abundant in feeder roots of peach seedlings in all treatments. From 88.1 to 94.0% of the feeder roots grown in soil at pH 5.6 to 7.2 had numerous vesicles and arbuscles (Table 2). In soil adjusted to pH 6.6 with $MgCO_3$, VA mycorrhizae were in only 77.6% of the roots.

Recovery of *Pythium* spp. from roots was positively correlated with increases in soil pH (Table 2). Only a few rootlets (1.2%-10%) of plants grown in soil with pH below 6.9 were invaded by *Pythium* spp. but increased to 16.2 and 33.7%, when the pH of soil was raised to 6.9 or 7.2. Most of the Pythium isolates were identified as *P. vexans* de By. or *P. irregulare* Buis., one was an unidentified *Pythium* sp. A few cultures of *Mortierella* spp. were also obtained from roots cultured on the medium used to isolate *Pythium* spp. Other fungi often isolated from feeder roots were *Cylindrocarpon* spp. and *Fusarium* spp. The greatest number of *Fusarium* spp. was isolated from roots grown in soil at pH 7.2 (Table 2).

Soil pH also affected propagule populations of *Pythium* spp. in soil (Table 3). Propagules of *Pythium* spp. per gram of dry soil increased from 20.8 and 24.0 at pH 5.6 to 368.9 at pH 6.9, about a 16-fold increase. Although populations of total fungi, bacteria, and actinomycetes did not differ significantly among the various pH treatments, total soil fungi and soil pH had a positive correlation, and populations of bacteria and actinomycetes and soil pH had a negative correlation (Table 3).

Criconemoides xenoplax and *Tylenchorhynchus claytoni* Steiner were the main nematodes in the soil. Only occasional *Meloidogyne* spp. larvae and *Xiphinema americanum* Cobb specimens were found. Populations of *C. xenoplax* in the soil before treatments ranged from 730 to 1,430, and averaged 912 per 150 cm^3 of soil. In December, shortly after the plants were inoculated, the populations of *C. xenoplax* were significantly higher when the soil was 6.4 or above (Table 4). In the March and April assays, the populations of *C. xenoplax* had increased in the control soil, and numbers of nematodes did not significantly differ.

DISCUSSION.—The results of this study indicate that susceptibility to *P. syringae* of peach seedlings grown in old orchard soil can be reduced when soil pH is raised after amendment with $CaCO_3$ or $MgCO_3$. Since both $CaCO_3$ and $MgCO_3$ gave similar results, the beneficial effect probably resulted from increased pH rather than Ca^{++} or Mg^{++} added to the soil.

The higher soil pH probably only indirectly increased survival of plants. Soil in orchard sites without peach tree short-life often has a pH as low as soil in sites with short-

life or decline (Weaver and Wehunt *unpublished*). Prince et al. (25) reported increased growth of peaches in pots of soil of pH 4.2 from an old peach site when the soil was limed, steam-sterilized, or fumigated. However, trees grew best in untreated nonpeach soil with pH 4.7.

The peach seedlings inoculated in this study were not damaged by bacterial canker or cold until they had received about 66% or 87% of the chilling required to break dormancy. A prolonged warm period followed by a sudden freeze also occurred before the appearance of stem damage. This result agrees with other reports (4, 24) that peach trees were susceptible to cold only after they had received most or all of the chilling necessary to break dormancy and were exposed to warm temperatures followed by below freezing temperatures. Since typical symptoms of bacterial canker occurred on the stems, and *P. syringe* was recovered from all but one of the diseased plants, *P. syringe* probably caused most of the damage. However, the uninoculated plants were probably injured by cold. Thus, cold damage and *P. syringae* may also have interacted on plants inoculated with the bacterium. Simultaneous cold damage and bacterial canker have been reported on peach trees (23, 28). Since *P. syringae* was isolated from one of the control plants in this test, the pathogen may have spread naturally, or control plants may have been contaminated accidentally.

We found that the growth of peach stems was similar in all treatments and was not related to susceptibility to *P. syringae*. This finding supports observations that peach trees succumb to short life, even though they appeared healthy and grew vigorously before going into dormancy (24).

The need for orchard peach trees to be predisposed before being injured by *P. syringae* has been recognized (5, 10, 21, 28). *Pythium* spp. have been shown by Lownsbery et al. (21) to increase susceptibility of peach trees to *P. syringae*. However, conflicting evidence has been reported for the role of *Pythium* spp. in the short-life problem (16, 17, 22). We found a strong positive correlation between soil pH and populations of *Pythium* spp. in the soil or in feeder roots. However, discoloration of feeder roots was similar in all treatments and was not related to populations of *Pythium* spp. or susceptibility of the plants to *P. syringae*. These results support the conclusion of Mircetich (22) that no direct relationship exists between peach tree short-life and the occurrence of *Pythium* spp. in soil or roots.

The nematode *C. xenoplax* is usually associated with peach trees in orchards with the short-life problem (6, 11, 17, 28). In pot tests, *C. xenoplax* either did not affect (30), or reduced (1, 21), growth of peach. In one test the nematode increased susceptibility to *P. syringae* (21). However, soil in these tests was usually steamed or fumigated before use. In the natural soil in our experiments, populations of *C. xenoplax* did not greatly increase during the 9-month test period. In the first 6 months after treatment, more *C. xenoplax* specimens were present in soil adjusted to the higher pH levels, but a few months later the nematode had passed peak populations, and no significant differences were found. Similar results were obtained by Lownsbery (20).

Gilmore (13) recently showed the importance of vesicular-arbuscular mycorrhizae in the growth and mineral uptake by peach seedlings. In our study, endotrophic mycorrhizae were abundant in feeder roots at all pH levels tested, but were significantly reduced in soil adjusted to pH 6.6 with $MgCO_3$.

Our results suggest that none of the differences in plant growth or in populations of bacteria, fungi, or nematode accounts for the reduction in susceptibility of peach seedlings to *P. syringae* when the soil pH was raised by liming. Thus, numbers of organisms is not a reliable index of potential damage.

Recent reports (3, 18) have shown that leachates from orchard soil containing peach roots reduced respiration of peach roots and increased susceptibility of peach seedlings to *P. syringae* much more than leachates from nonpeach soil. These results led Chandler and Daniell (3) to postulate that peach trees planted on old peach sites take up some water soluble substance and are predisposed to bacterial canker. Peach trees grown on old peach land have also been shown to accumulate greater quantities of certain minerals during dormancy than trees grown on new land (8). These reports warrant further studies of how soil from old peach sites affects the physiology of peach trees and may alter their susceptibility to *P. syringae*.

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