

Influence of Antagonists and Controlled Matric Potential on the Survival of *Pseudomonas solanacearum* in Four North Carolina Soils

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ABSTRACT

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Large numbers of microorganisms antagonistic to *Pseudomonas solanacearum* were detected in each of two suppressive soils (Worsham and Arapahoe) and two conducive soils (Norfolk and Torhaunta). In the suppressive soils, highest populations of antagonistic bacteria were detected in Worsham soil and the highest populations of antagonistic fungi and actinomycetes were in the Arapahoe soil. Lowest populations of antagonists were associated with the Norfolk soil. Soil moisture significantly affected reproduction and survival of *P. solanacearum* in

unsterile soils, regardless of soil type; colony counts increased within 7–10 days of introduction into the soil at the highest soil moistures (from flooded to –1 bar), but did not increase in drier soils (from –5 to –15 bars). The most favorable soil moisture for survival of *P. solanacearum* was –0.5 to –1 bars. Decline of *P. solanacearum* was more rapid when added to the four soils 60 days after imposing moisture regimes than when added on day 1. Soil type, which influenced soil moisture, determined the size of antagonistic populations, which in turn affected the survival of *P. solanacearum* in soil.

Additional key words: biological control, soilborne pathogens.

Pseudomonas solanacearum, E. F. Smith, a soilborne pathogen, persists in many different soils around the world (2,16). Survival from 2 to 10 yr in fallow soil has been reported; whereas, in other soils, its population declines rapidly despite the presence of susceptible crops (2,7,10). Generalizations about soil factors associated with survival of the pathogen are difficult because workers have not characterized the soils involved; nevertheless, alternative hosts, antagonists, and soil moisture clearly affect survival (3,11). Survival of *P. solanacearum* is most efficient in wet (but well drained) soils. Survival is affected adversely by soil desiccation and flooding (2,9,16,30). However, survival studies under controlled soil moisture have not been conducted (3).

P. solanacearum survived from season to season in a Norfolk loamy sand and Torhaunta fine loamy sand but failed to overwinter in a Worsham sandy loam and Arapahoe coarse loamy sand unless the soils had been fumigated previously (25). We suspect that biological and physical factors, especially soil moisture, influenced survival. In Georgia, *P. solanacearum* survived better in the lighter-textured Marlboro loamy sand than in the heavier Appling sandy loam (21).

The objectives of this study were to determine the effect of soil moisture on the survival of *P. solanacearum* and antagonistic soil microorganisms in four North Carolina soils.

MATERIALS AND METHODS

Inoculum of a virulent, fluidal strain of *P. solanacearum* isolate K 60, race 1, biotype 1 was produced by transferring a single virulent colony to a flask of a liquid, semisynthetic medium (SSM) (14) without CaCO₂. Cultures were grown for 72 hr at 30 C on a shaker; harvested aseptically by centrifugation at 5,000 g; washed twice in sterile, deionized water; and then used to infest soil. Four

North Carolina soils described earlier were used in this experiment (25). Norfolk sandy loam and Torhaunta fine loamy sand favored survival of *P. solanacearum* under field conditions and Worsham sandy loam and Arapahoe coarse loamy sand did not (25). These soils were collected from the field 3 days prior to initiation of the experiments. The soils differed widely in water holding characteristics (Fig. 1). The reported drainage characteristics are: Norfolk, well drained; Torhaunta, moderate well drained; Worsham, poorly drained; and Arapahoe, excessively drained (19).

Assays for antagonistic fungi, bacteria, and actinomycetes. Antagonistic fungi, bacteria, and actinomycetes from the four soil types were enumerated from counts on plates seeded with 10-fold serial dilutions, using 10-g soil samples in 90 ml of sterile deionized water, replicated six times (15). Assays were done at weekly intervals. One-tenth milliliter from each dilution was plated on the surface of each of the following media: acidified potato-dextrose agar (APDA) (33) and water agar (WA) (33) for fungi; Difco nutrient agar (NA) (6), Difco nutrient agar amended with 2% glucose (GNA), and soil extract agar (SEA) (15) for bacteria; and a chitin agar (CA) (20) and starch-casein agar (S-CA) (15) for actinomycetes. Plates from each soil dilution were incubated at 25 C except the SEA plates, which were placed in an anaerobic chamber and purged three times with 20% CO₂ and 80% N₂ to isolate anaerobes. Plates of GNA and NA after 3 days; APDA and S-CA after 7 days; and WA, SEA, and CA after 14 days were moved to refrigeration (5 ± 2 C). On day 15, all plates were exposed to chloroform fumes for 4 hr to kill the organisms, then were aerated aseptically for 3–5 hr. Afterwards, plates were seeded with a thin layer of SSM with 0.3% agar containing *P. solanacearum* at 2.5 × 10⁷ colony-forming units (cfu) per milliliter and incubated for 25 hr at 30 C. Colonies were considered to be antagonistic if surrounded by clear zones. The experimental design was a split plot and the data were analyzed by analysis of variance.

Assays for lytic microorganisms, protozoa, bdellovibrios, and bacteriophage. Lytic microorganisms were enumerated by amending water agar with a 1:1 mixture of live and heat-killed cells of *P. solanacearum* (approximately 10¹⁰ cells per milliliter). This medium was poured into plates containing 1 ml from each soil dilution (12). The plates were incubated 3 days at 25 C and the

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number of colonies surrounded by clear zones was counted. Protozoa were enumerated by the Singh ring test as modified by Habte and Alexander (12). Protozoa were killed in formalin and counted with a microbial counting chamber and microscope. The double-layer technique of Stolp and Starr (31) was used to quantify bdellovibrios while bacteriophages were enumerated by the method of Crosse and Hingarani (4) except that Hayward's medium (13) was used as the bottom layer.

Assays for chemical toxicity. Chemical toxicity of the soil to *P. solanacearum* was assessed with 0.1 M sodium tartrate and deionized water to leach soils (15). The leachates were used in place of distilled water to prepare SSM; the resulting media were then seeded with *P. solanacearum* and incubated at 30 C. Growth rate was monitored by measuring changes in optical density at 540 nm by using a colorimeter (Baush and Lomb Spectronic 20).

Controlled soil moisture. *Experiment 1.* Soil moisture chambers were Mason jars (1 L) covered with rubber-lined jar lid and dome rings. To allow for gas exchange with the outside air with minimum loss of soil water, a cotton plugged glass tube was inserted through the lid and covering with a moisture retaining, gas-permeable plastic film (Stretch 'n' Seal; Imperial Oil Limited). Chambers were autoclaved at 120 C for 15 min before soil was added. The chambers were about half-filled with 500 g of soil, previously brought to a desired matric potential, and retained in sterile, soil-moisture chambers. Matric potentials were established and controlled among all four soils by using a pressure-membrane or pressure-plate apparatus to establish 0, -0.3, -0.5, -1.0, -5, and -15 bars matric potential (18). The soils were allowed to equilibrate in the apparatuses for 24 hr. Several daily runs were required of the apparatuses to accumulate sufficient soil for the different soil moistures-matric potentials to fill the chambers. Therefore, upon removal of each quantity of soil from the apparatuses with a metal spatula, it was transferred immediately to the sterilized soil moisture chambers to minimize evaporative drying until the chambers were established 10 days later. Flooded soil was established by covering saturated soil with 5 cm of sterile deionized water. The soils from the various runs were blended by shaking and stirring, then were transferred quickly to the Mason jars with a spatula.

Field soil was infested with *P. solanacearum* by aseptically spraying 50 g of air-dried soil with the amount of water containing inoculum necessary to bring the sample to the same matric potential as that already established inside the chambers. Infested soil was then transferred to the chambers and mixed thoroughly with the larger volume of soil. The final density of *P. solanacearum* in the chambers was approximately 5×10^5 cfu/g dry soil. Uninfested field soils served as controls.

The chambers were arranged in a completely random design of three replications in a dark incubator at 30 C. On the date of infestation, and at weekly intervals thereafter, three 10-g soil samples were removed. One sample was used to determine soil moisture gravimetrically (22) and the other two were diluted serially (15) in 90 ml of sterile deionized water. Assays for suppressive microorganisms were conducted as indicated above. Densities of the virulent fluidal colony type of *P. solanacearum* were monitored weekly on an agar-solidified selective medium (FSM) described elsewhere (24). Data were analyzed by using analysis of variance.

Experiment 2. In another experiment, the pathogen was added to one-half of the chambers when the soil moisture regimes were established and to the other half of the chambers 60 days later. This experiment was designed to determine if *P. solanacearum* would survive to a greater or lesser extent once the soil ecosystem had time to stabilize.

Experiment 3. A greenhouse experiment was conducted to separate the effect of soil moisture from changing populations of soil microorganisms on the survival of *P. solanacearum*. Soil moisture chambers were plastic cups (1 L) approximately three-fourths full of either leached, steamed (15), or unsteamed soil (100 g) and covered with a double layer of Stretch 'n' Seal secured with a rubber band. To prevent sudden changes in temperature, the chambers were buried in a commercial potting mixture plus

vermiculite so that their tops were exposed. This experiment was designed as a randomized, complete block with three replications.

Steamed and unsteamed soils were infested with *P. solanacearum* at approximately 5×10^5 cfu/g dry soil by spraying the inoculum into each soil while agitating it with a spatula. The inoculum had been diluted with the amount of water necessary to establish the same soil moisture levels maintained in the previous experiments. All soils had been air dried to beyond the permanent wilting point prior to being infested. The amount of water added was calculated, based on the existing matric potential of each soil and interpolations were made from the soil moisture retention curves (Fig. 1). During the experiment, the moisture chambers were weighed and water was replenished by spraying the soil and mixing the amount of water needed to reestablish desired soil moisture. Soil was sampled for *P. solanacearum* by using the FSM every 15 days during the first 60 days and every 30 days thereafter for 7 mo. Survival for the date was considered positive if at least 1 cfu of *P. solanacearum* was detected.

Addition of antagonist to soil. Autoclaved, steamed, and unsteamed Norfolk sandy loam were infested with *P. solanacearum*; *Trichoderma viride*, *Fusarium roseum*, *Pseudomonas* sp., *Bacillus* sp., and *Streptomyces* spp.; which had been isolated during the previous studies and had shown evidence of activity inhibitory to *P. solanacearum*. These isolates were stored at room temperature on the medium used to isolate them from soil. Soils at 0, -0.5, and -5 bars matric potential were placed in the soil moisture chambers and infested with *P. solanacearum* at 2.5×10^7 cfu/g dry soil, and then one-half of each soil was infested with 1 ml of a turbid suspension of one of the candidate antagonists. The chambers were placed at 30 C in a dark incubator and assayed weekly for 12 wk for *P. solanacearum*, on FSM, and for the antagonists, on the appropriate assay media described for the suppressive agents.

RESULTS

Antagonists in field soils. Large numbers of different microorganisms antagonistic to *P. solanacearum* were detected on appropriate agar plates from all soils as determined by the double-layer technique. In the suppressive soils, the highest numbers of antagonistic bacteria were detected in Worsham soil and highest counts of antagonistic fungi and actinomycetes were associated with Arapahoe soil (Table 1). Lowest numbers of antagonists were detected in the Norfolk soil. Bacteriophages were found only in the Norfolk soil. Bdellovibrios were present in Worsham soil but were not detected regularly. Highest counts of both bacteriophages and bdellovibrios were found 2 wk after the addition of *P. solanacearum*, but populations of these predators declined rapidly. Counts of microorganisms lytic to *P. solanacearum* were very erratic and were isolated with equal frequency from all four soils.

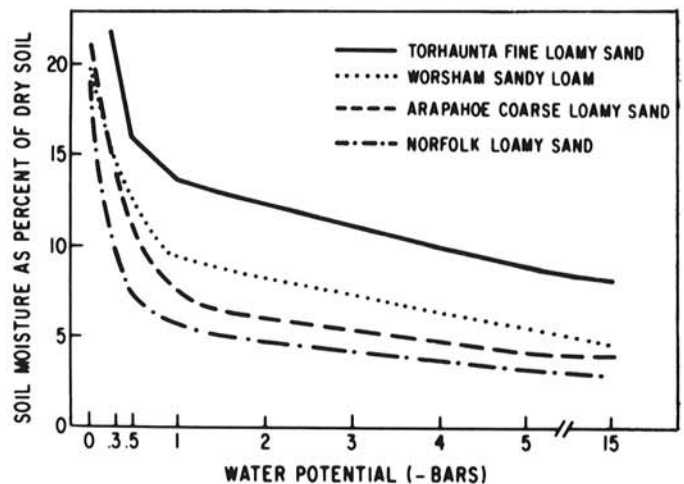


Fig. 1. Soil moisture curves of four North Carolina soils as determined by the pressure-membrane and pressure-plate technique.

Protozoa were abundant in all four soils shortly after the addition of *P. solanacearum*. Counts of 10^4 to 10^5 protozoa and amoeba per gram of soil were common 2 wk after infestation, but counts were below 10^2 cells per gram of soil when not infested with *P. solanacearum*. Counts between soils were not different ($P = 0.05$).

Sodium tartrate and deionized water leachates from compatible and suppressive soils supported growth of *P. solanacearum* equally well ($P = 0.05$).

TABLE 1. Kind and numbers of organisms antagonistic to *Pseudomonas solanacearum* in four soils

Soil type	Antagonists soil		
	Bacteria	Fungi	Actinomycetes
Norfolk sandy loam	290 a ^z	780 a	1,100 ab
Torhaunta fine loamy sand	6,100 b	160,000 b	48,000 b
Arapahoe coarse loamy sand	140 a	1,200,000 b	2,200,000 c
Worsham sandy loam	330,000 c	260 a	370 a

^z Counts followed by the same letter in the same column are not significantly different, $P = 0.05$, according to Duncan's new multiple range test.

Effects of soil moisture on *P. solanacearum* and populations of antagonists. Populations of *P. solanacearum* in unsterile soils maintained at different matric potentials characteristically increased initially and then gradually declined (Fig. 2). Regardless of soil type, colony counts increased within 7–10 days in soils flooded or moistened to at least -1 bar. Highest populations were found in saturated (but not flooded) soils (0 bars). Generally, multiplication of the pathogen was not detected in soils at -5 to -15 bars matric potential. Colony counts declined rapidly in all soils either flooded or held at -15 bars. However, population trends for *P. solanacearum* were not consistent among the various soils held at matric potentials between 0 and -5 bars. Statistical analysis of the populations on day 35 gave a significant soil \times soil moisture interaction ($P = 0.05$). Generally, across soil types, high populations were maintained the longest at -0.5 bars. *P. solanacearum* survived at the highest populations for the longest period in Norfolk and Torhaunta soils held at -0.5 to -1 bars soil water potential. In contrast, no consistent pattern was detected with the other two soil types. Highest sustained populations during the test period were detected in Arapahoe soil under wet conditions (0 to -0.5) compared to Worsham soil where drier conditions (-0.5 to -5) yielded highest counts for the longest period.

Preliminary assays of suppressive agents in the soil moisture chambers indicated populations of protozoa increased rapidly in

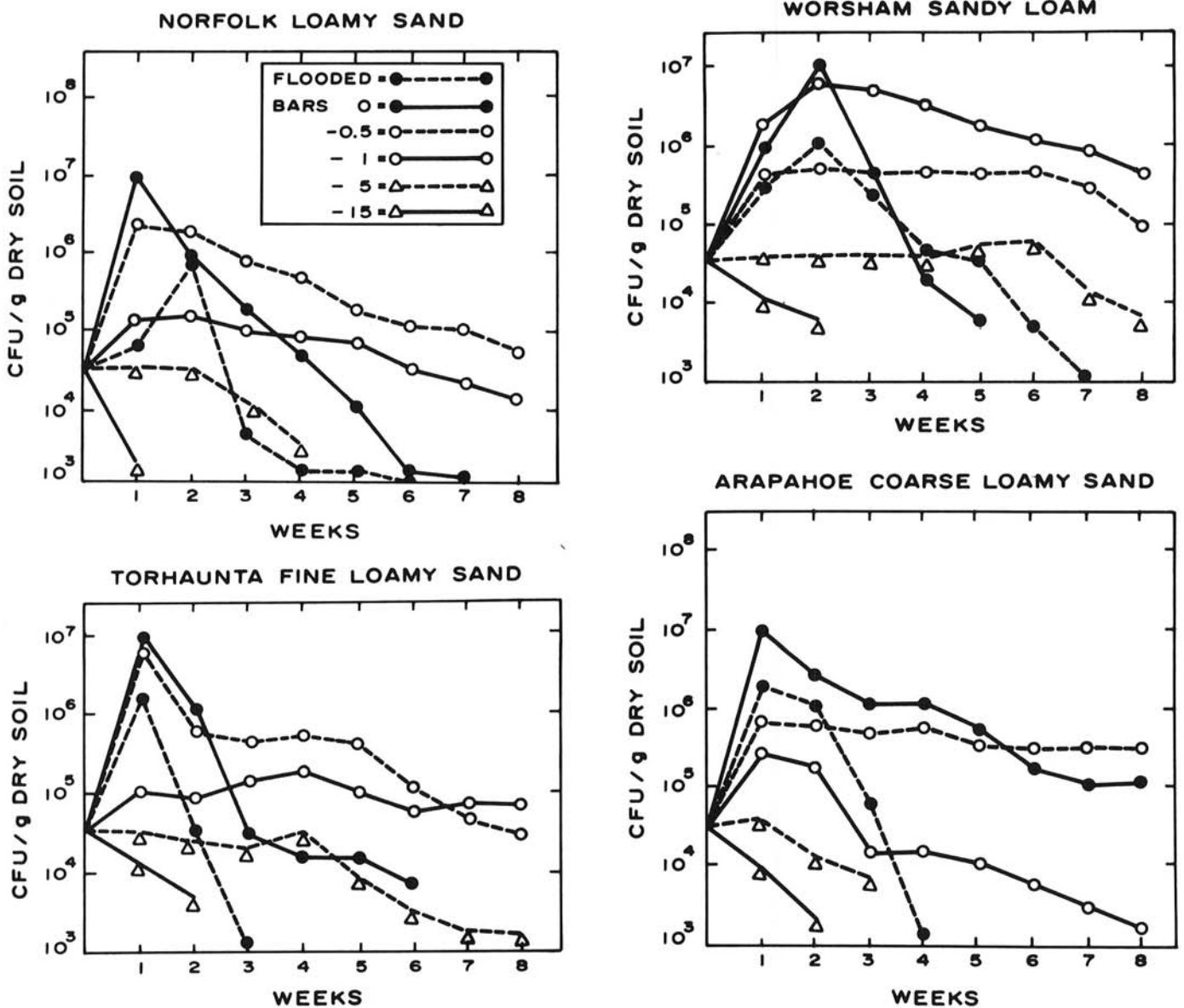


Fig 2. Effect of constant soil moisture on the survival of *Pseudomonas solanacearum* (fluidal colony type) in four North Carolina soils for an 8-wk period.

soils infested with *P. solanacearum* and flooded or drained to -0.5 bars. However, bacteriophage and bdellovibrios counts were variable and soil extracts were nontoxic.

Antagonists to *P. solanacearum* were greatly affected by soil moisture (Fig. 3). Antagonistic actinomycetes were most numerous in dry soils, while antagonistic bacteria were most numerous in wet soils. Highest counts of antagonistic actinomycetes were found in Arapahoe soil at matric potentials drier than -0.5 bars. Highest counts of antagonistic bacteria were associated with Worsham soil at matric potentials wetter than -0.5 bars. Numbers of antagonistic fungi were highest in Norfolk and Torhaunta soils held between -0.5 and -5 bars and in Arapahoe and Worsham soils between -5 and -15 bars, but differences were not associated with suppressive or conducive soils. *Penicillium*, *Aspergillus*, *Trichoderma*, and *Fusarium* spp. were the most frequent fungi observed to inhibit *P. solanacearum* in agar plates.

In a greenhouse experiment designed to evaluate the effects of soil moisture on how long *P. solanacearum* could be detected in steamed and unsteamed soils, the length of the detection period was improved by steaming only in certain soil-soil moisture regimes (Table 2). The greatest length of the detection period in steamed soil occurred in the suppressive soils. In Arapahoe soil, the length of detection was improved significantly in steamed compared to unsteamed soil -1 to -5 bars while in Worsham soil steaming improved the detection period in soils at 0 to -0.3 bars matric potential. No differences were observed in length of detection period for *P. solanacearum* among soils or steam treatment at -0.5 bars.

Generally, survival was poorest in all soils if held flooded, saturated, or at -5 to -15 bars soil moisture for 60 days before adding *P. solanacearum* compared to the same soils moistened to the respective water potential 1 day before addition of *P. solanacearum* (Table 3). Conversely, survival was enhanced in soil held 60 days at -0.3 to -0.5 bars prior to infesting. In Arapahoe and Norfolk soils, at -1 bars, longevity was reduced significantly by adding the pathogen 60 days later.

Demonstration of antagonism. *Trichoderma viride*, *Fusarium roseum*, *Pseudomonas* sp., *Bacillus* sp., and two *Streptomyces* spp.

readily colonized autoclaved and steamed soils. *P. solanacearum* could not be detected within 7 days from soils infested with one of these antagonists, except where the actinomycetes had been added, in which case the pathogen was detected 9 wk at 0 bars but only 3 wk at -5 bars. *P. solanacearum* was detected in soils without the antagonists for 12 wk but mostly small butyrous colonies of the avirulent type (14) appeared in autoclaved soil. In unsterile soil, the level of antagonists recovered was not greater in soil amended with the antagonist than in unamended soil. The pathogen persisted equally well in antagonist-amended and unamended unsterile soils.

DISCUSSION

P. solanacearum survived equally well in suppressive and conducive soils within the range of soil moisture from -0.5 to -1 bars. Within that range, antagonists existed, but no one group

TABLE 2. Effect of soil moisture and soil type on the survival of *Pseudomonas solanacearum*^a in steamed and nonsteamed soils

Soil type	Treatment	Longevity (days) at soil moisture (bars) ^b					
		0	-0.3	-0.5	-1	-5	-15
Norfolk sandy loam	Steamed	120	190	210	210	180	15
	Unsteamed	80	170	210	210	120	15
Torhaunta fine loamy sand	Steamed	90	180	210	190	180	20
	Unsteamed	45	150	210	210	160	45
Arapahoe coarse loamy sand	Steamed	110	210	210	140	140	15
	Unsteamed	60	190	210	90	45	15
Worsham sandy loam	Steamed	90	180	210	210	210	30
	Unsteamed	45	80	210	210	180	30

^a Initial infestation, 5×10^5 cells per gram of soil.

^b Total length of test was 210 days. LSD ($P = 0.05$) for comparing any pair of means is 33. Survival was considered positive if one colony of *P. solanacearum* was recovered on the date.

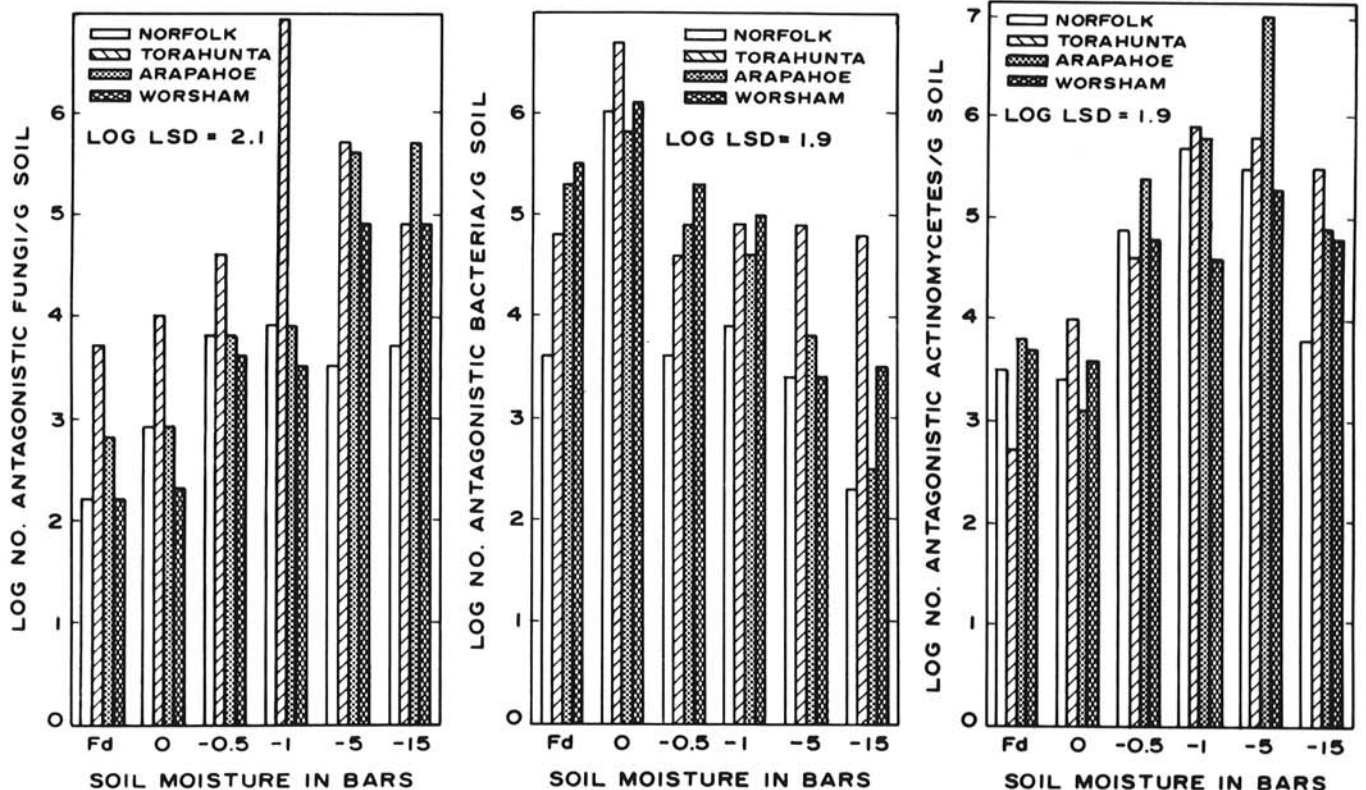


Fig. 3. Effects of soil moisture and soil type on the number of fungi, bacteria, and actinomycetes antagonistic to *Pseudomonas solanacearum* as determined by the double-layer technique. Fd = flooded.

dominated. However, in drier soils antagonistic actinomycetes dominated while in wetter soils bacteria dominated. Poorest survival of *P. solanacearum* occurred regardless of soil type in flooded or saturated soils and in soils at -15 bars. In a comparison of survival in soils maintained 1 day or 60 days at the respective water contents, populations of *P. solanacearum* decreased more rapidly in soils flooded, saturated, or held at -5 to -15 bars for 60 days compared with only 1 day. Conversely, populations of *P. solanacearum* increased in all soils held at -0.3 to -0.5 bars. These findings suggest antagonistic microbes are associated with the decline of *P. solanacearum* in these soil with soil moisture as a regulating factor.

Predators and parasites (such as protozoa, bacteriophages, and bdellovibrios) are unlikely candidates accounting for the suppressive nature of these soils. Counts of protozoa and bdellovibrios in compatible and suppressive soils were generally similar. Bacteriophages were recovered only from Norfolk soil, in which *P. solanacearum* survives well. Although protozoa probably reduce populations of *P. solanacearum* in soil (22), their predation does not account for the poor survival of the pathogen in these soils. In addition, even though amendment with 10 ppm of actidione eliminated most protozoan activity in these soils, rapid decline of *P. solanacearum* continued (W. C. Nesmith, unpublished). Apparently, chemical toxicity does not account for the suppressive nature of these soils either, since the pathogen increased substantially during the first 2 wk in all soils where the water potential was below -1 bar, and the bacterium also grew well in soil leachates. Instead, our data suggest that bacteria and actinomycetes may be the major antagonists to *P. solanacearum* in soil because highest numbers were associated with the suppressive systems (Table 1). Others (8,26,32) have reported that antagonism to *P. solanacearum* is a major reason the pathogen declines faster in top soils than in subsoils and in flooded versus nonflooded soils. Tanaka and Noda (32) demonstrated that adding chitin to subsoils caused rapid decline of *P. solanacearum* due to antagonists. Generally, the addition of chitin to soil causes a substantial increase in numbers of actinomycetes (11). The mechanism of antagonism is unclear because soil extracts did not contain toxic factors. Still, antibiosis has been considered to be the mechanism of antagonism (11,27). Thus, by a process of elimination, it is suspected that competition is the major form of antagonism in suppressive soils.

High soil moisture is the factor most consistently associated with persistence of bacterial wilt worldwide (8,16,26). However, the nature of this relationship is not understood, probably because soil moisture has not been critically controlled (3). Gondo and Amimura (8), Okabe (26), and Tanaka and Noda (32) investigated the effects of soil moisture on the reproduction and survival of *P. solanacearum*. They found that the pathogen reproduced in moist soils between 15 and 80% water-holding capacity. However, no

reports have been presented in which soil moisture was adequately controlled or expressed in reproducible terms since percent water-holding capacity is not equivalent to soil matric potential from soil to soil (18). In our experiments, soil matric potential was established and held without appreciable changes for the 270 days of the experiment; and we measured soil matric potential which is a universal value with reproducibility from soil to soil (18). However, matric potential probably changed occasionally due to some condensation on the jar surface, but adequate time was provided for reestablishment of equilibrium.

Reproduction of *P. solanacearum* was detected at soil moistures from flooded to -1 bar in all soils that we tested. This was surprising since these soils presumably were low in available carbon and nitrogen. Highest populations were detected at 0 bars. Population increases were not detected when soils were held at or below saturation, rather they declined rapidly. This supports previous observations that the pathogen is sensitive to desiccation and is favored by wet soils (2,7,16,30).

Survival of the virulent, fluidal colony type also was influenced by soil moisture. However, survival of the pathogen appeared to be equally dependent upon the soil used. Thus, other soil physical, chemical, or biological factors are surely involved. Our attempts to eliminate other biological factors by using sterile soil were unsuccessful. The avirulent colony type was recovered. Nevertheless, all unsterile soils could be converted from a decrease in survival of *P. solanacearum* to an increase in its survival by changing soil moisture levels. Generally, in all the tested soils the pathogen survived well at -0.5 to -1 bars, except slightly wetter soils favored pathogen survival in the normally arid Arapahoe soil.

P. solanacearum did not survive well in all soils if flooded or held at -15 bars. This is in agreement with the work of others and indicates that the pathogen is sensitive to prolonged flooding and dry fallow (2,9,22,31). We could not detect virulent, fluidal colony types after about 60-70 days, and others report that a 90-day inundation is adequate for control (16). The suppressive Worsham soils are poorly drained at the site and remain saturated most of the winter. This may explain the poor survival of *P. solanacearum* at the site, even though adequate disease development can be created by annual infestation with the pathogen (25). Loss of the pathogen in flooded soils is usually attributed to antagonism; we find no reason to disagree, since inundation for 60 days prior to infestation with the pathogen greatly reduced its longevity in our tests (Fig. 2, Table 3).

The suppressive Arapahoe soil dried rapidly in the field and was near the permanent wilting point at the 10-cm depth within 2 wk under bare fallow (unpublished). North Carolina potato growers recognized the problems with bacterial wilt on this soil compared to nearby soils as early as 1940 (L. W. Nielsen and F. A. Todd, personal communication). However, this soil is typical of only a small portion of lower coastal plain soils in North Carolina (19). Such data suggest that factors antagonistic to *P. solanacearum* may develop even before soils become so dry that desiccation is directly lethal to the pathogen.

The Norfolk and Torhaunta soils that we used are well drained yet have excellent water retention characteristics due to silt, clay, and organic matter (19). Except in the top few centimeters, these soils seldom dry to the wilting point, and are flooded for no more than a few hours after a heavy rain. Based on our data, these soils should support reproduction and survival of *P. solanacearum* much of the time. The water holding capacities of these soils are typical of those of many coastal plain and Piedmont soils in which bacterial wilt is a perennial problem in North Carolina.

Compatible soils apparently provide a favorable physical and biological environment for the pathogen to persist until conditions (suitable hosts) are favorable for development and multiplication. Likewise, suppressive soils possess a physical environment that encourages high populations of microbes antagonistic to *P. solanacearum*. Soil physical factors and water supply affect the soil moisture that determines the antagonistic level.

Survival of *P. solanacearum* was greatly reduced in unsteamed compared to steamed soils. Exclusive of -15 bars, survival in steamed soils was shortest in flooded soils which indicates that

TABLE 3. Effect of soil moisture and soil type on the survival of *Pseudomonas solanacearum* when soil was infested with the pathogen on the date soil moisture was established versus 60 days later

Soil type	Infestation date	Flooded	Longevity (days) at soil moisture (bars) ^a					
			0	-0.3	-0.5	-1	-5	-15
Norfolk loamy sand	1	80	80	240	270	210	160	30
	60	7	7	270	270	110	22	7
Torhaunta fine loamy sand	1	70	80	130	190	220	170	70
	60	5	40	160	170	230	120	7
Arapahoe coarse loamy sand	1	90	120	190	200	70	50	25
	60	30	60	220	220	55	17	7
Worsham sandy loam	1	80	35	160	250	240	160	20
	60	27	25	130	210	250	90	12

^aTotal length of test was 270 days. LSD ($P = 0.05$) for comparing any pair of means is 44. Survival was considered positive if one colony of *P. solanacearum* was detected on the date.

flooding alone is detrimental to *P. solanacearum*. Loss of virulence in broth culture was reported due to motility and aerotactic response of avirulent cells compared to absence of motility in avirulent cells (17). A similar phenomenon may operate in flooded soils (29). Numbers of avirulent cells increased with time in all soils held above -1 bar soil matric potential, but most rapid increases were usually observed in flooded soils, especially in autoclaved or steamed soils.

The survival mechanism of *P. solanacearum* in soil is unknown. Ramos (28) hypothesized that the pathogen enters a resting phase because the doubling rate decreased substantially. Our data indicate that the pathogen multiplies in compatible soil systems then levels off at about 10^3 cfu/g, although detection is difficult. These observations may support the hypothesis that the organism enters a resting or resistant phase (28). Our previous findings (25), as well as those of the present study, demonstrate that antagonism and soil moisture are major reasons for poor survival of *P. solanacearum* in certain soils. Since it is suspected that competition is the major form of antagonism in suppressive soils, investigations should be designed to determine which competitive characteristics (especially those governed by soil moisture) of the resting population differ from those of the more rapidly declining phase.

Races 1 and 3 of *P. solanacearum* survive in many soils without a host (1,5,25,28) and apparently have evolved sufficient survival mechanisms to persist in compatible soils, but nevertheless are sensitive to antagonists in suppressive soils. Because the suppressive and compatible conditions appear to be governed by soil type and soil moisture regime, immediate application of these findings may be possible. If these findings are general in nature, knowing the soil type and soil moisture retention characteristics could allow growers to make wiser use of crop management and breeders could select better nursery sites.

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