Population Dynamics and Survival of *Xanthomonas campestris* in Soil in Citrus Nurseries in Maryland and Argentina

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ABSTRACT

Graham, J. H., Gottwald, T. R., Civerolo, E. L., and McGuire, R. G. 1989. Population dynamics and survival of *Xanthomonas campestris* in soil in citrus nurseries in Maryland and Argentina. Plant Disease 73:423-427.

The population dynamics and survival in soil of nursery strains of *Xanthomonas campestris* causing citrus bacterial spot in Florida (Xc) and strains of *X. c.* pv. *citri* causing Asiatic citrus canker (Xcc-A) were evaluated in citrus nurseries under quarantine in Maryland and in Argentina, where citrus canker is endemic. In Maryland, Xc and Xcc-A were recovered from the soil under infected nursery seedlings of Swingle citrumelo when the soil was relatively moist ($\psi \geq -30$ cbar) but not when it was drier ($\psi < -100$ cbar). The pathogens were not detected on leaves of adjacent uninfected trees or in the soil under them. The populations of Xc and Xcc-A were generally lower in soil than on leaves with lesions and on symptomless leaves from diseased plants. In Argentina, Xcc-A was detected in a sandy soil in grapefruit and sweet orange nurseries with disease proportions of 0.97 and 0.89, respectively. Fluctuations in soil populations were correlated with rainfall, soil moisture, and air temperature, as well as leaf populations. After the removal of infested plants to simulate eradication, Xcc-A could not be recovered after 21 days from either nursery site. It appears that Xcc-A and Xc have very limited survival capability in subtropical soils.

Additional keywords: environmental effects

Epidemics of two foliar diseases of citrus have been identified in Florida since 1984 (7,16). In 1984, a leaf, twig, and fruit spot caused by unique strains of *Xanthomonas campestris* (Pammel) Dowson was discovered in a citrus nursery (16). These strains have been called *X. c.* pv. *citri* (Hasse) Dye strain E (2,5,9) and Florida nursery strains (8) and are here designated Xc. The Asiatic type of citrus canker (type A), caused by *X. c.* pv. *citri* strains of group A (Xcc-A), was detected in 1985 and 1986 at residences and since then in two commercial groves on the west coast of Florida (16). Unlike citrus canker, with its corky,

erumpent lesions, the nursery disease characteristically has flattened lesions, and Xc strains are serologically and genetically distinct from Xcc-A (2,9,16). On the basis of these comparisons, the nursery disease has been termed citrus bacterial spot (5,6,7). Currently, citrus bacterial spot strains have been isolated from over 30 nurseries and three groves in Florida. In all but two situations, where defoliation was used, plants infected with citrus bacterial spot or citrus canker were eradicated (16).

Several *Xanthomonas* spp. survive in soil in debris of diseased plants (10,15,17). In previous research in Florida and Argentina, Xcc-A survived up to 6 mo in dry leaves on the soil surface but less than 3 mo if the leaves were buried in moist soil (8). In Maryland, Xc was recovered from soil under diseased plants at populations occasionally as high as those on the

leaves (5).

The saprophytic potential of Xcc-A apart from plant material has not been conclusively demonstrated. In Japan, the bacterium was recovered from artificially infested field soil for up to 5 mo during the fall and winter but only 2 mo in the spring (3,4). Similarly, in the spring in Brazil, Xcc-A survived 35 and 56 days in naturally infested sandy and clayey soils, respectively (12). Thus, survival in soil may be influenced by climate and season as well as soil moisture and soil type.

The purpose of these studies was 1) to evaluate the relationship between epiphytic populations on citrus leaves, environmental conditions, and the population dynamics of Xc and Xcc-A in soil and 2) to determine whether Xcc-A survives in soil after the eradication of citrus nursery plants severely affected by citrus canker. Quarantine restrictions in Florida have prohibited field research on citrus canker and citrus bacterial spot (7). Therefore, studies were conducted under quarantine in field plots in Maryland and in Argentina, where the soils and climate are similar to those in Florida and citrus canker is endemic.

MATERIALS AND METHODS

Field plot locations. Studies were conducted at the USDA-ARS Foreign Disease and Weed Research Laboratory, located at Fort Detrick, Frederick, Maryland (Frederick, 1986); the USDA-ARS Agricultural Research Center, Beltsville, Maryland (Beltsville, 1987); and the INTA Citrus Experiment Station, Concordia, Entre Rios, Argentina (Argentina, 1987).

Recovery from plants and soil in nursery epidemics. At Frederick, two citrus seedling plots were established to

simulate nursery conditions in Florida. Each plot consisted of 11 rows of 45 seedlings (20–30 cm tall) planted in Sassafras gravelly sandy loam (sand, 63%; silt, 20%; and clay, 17%; pH 5.5) with spacings of 15 cm within the row and 75 cm between the rows. In each nursery, a row of diseased Swingle citrumelo (*Citrus paradisi* Macf. × *Poncirus trifoliata* (L.) Raf.) provided a line source of inoculum to test the spread of the pathogen through the plots (Gottwald, *unpublished*). Seedlings in the adjacent rows in the Xcc-A plot were *P. trifoliata* cv. Flying Dragon, and in the Xc plot were Swingle citrumelo. The cultivars used have been associated with citrus bacterial spot epidemics in nurseries and are known to be susceptible to both diseases (16).

The strains of Xcc-A and Xc were XC62 (Civerolo) from Japan and X4600 (Gottwald; J. W. Miller, DPI, X85-X4600-1) from an infested citrus nursery in Florida, respectively. To detect whether spread occurred between the two plots, which were separated by only 20 m, a marked strain of X4600 was derived as a spontaneous mutant (X4600RS) on nutrient agar amended with rifampicin and streptomycin. Strain X4600RS could be identified if cross-contamination by strain XC62 occurred.

Inocula of XC62 and X4600RS were grown in nutrient broth (for 24 hr at 25 C), centrifuged, and resuspended in sterile distilled water. A cell suspension of each strain (approximately 10^8 cfu/ml, determined spectrophotometrically) was sprayed onto trays of 100 Swingle citrumelo seedlings until runoff. The trays of seedlings were covered with plastic for 3 days to maintain leaf wetness and then incubated for 30 days under greenhouse conditions. Plants with a disease incidence of about 20% (number of diseased leaves per total number of leaves, multiplied by 100) were planted in the plots in June 1986.

Diseased and asymptomatic leaves were sampled monthly. There were three replicate collections for each treatment. Single leaves, collected from three inoculated and three uninoculated plants in each plot, were bulked and washed in 20 ml of 0.075 M phosphate buffer (pH 7.0) plus 0.1% peptone (13) and shaken for 1 hr. From each sample, 0.1-ml aliquots of the wash suspension and 10-fold serial dilutions were spread on single plates of two of the following three media: Tween medium C (13) for Xcc-A and Xc; KCB medium, containing nutrient agar (23.0 g/L) and glucose (0.1 g/L) (NGA) plus kasugamycin (16.0 mg/L), cephalexin (16 mg/L), and Daconil 720 (12.0 mg a.i./L) for Xcc-A; and NGA plus rifampicin, streptomycin, and cycloheximide (each 100 mg/L) for Xc. The plating efficiency of the selective media for the pathogens from leaves was greater than 90% of that of NGA. The

area of washed leaves was determined with a leaf area meter. Leaf populations were calculated as the mean of the colony counts on the two assay media and were expressed as colony-forming units per square centimeter of leaf area.

Soil under inoculated and uninoculated plants was sampled when the leaf samples were collected. Each sample consisted of a total of about 4 g (fresh weight) collected from the top 1.0-cm layer of soil at the four cardinal points within 10 cm of the trunk of each seedling. The samples were thoroughly mixed, and 1.5-g subsamples were suspended in 100 ml of sterile phosphate buffer plus peptone in 250-ml flasks and shaken for 1 hr. The soil was allowed to settle for about 15 sec, and the supernatant diluted and plated as described above. Four subsamples of fresh soil composited from all of the sample sites were dried at 105 C for 48 hr to determine soil moisture content. Gravimetric moisture content was converted to soil water potential (soil ψ) by means of a previously derived soil moisture curve (Graham, *unpublished*). Soil bacterial populations were expressed as colony-forming units per gram of soil (dry weight).

To determine the efficiency of the KCB and Tween C semiselective media for the detection of Xcc-A and Xc in the presence of nonsterile soil, bacteria were added to 1-g samples of moist sandy loam soil suspended in 100 ml of sterile phosphate buffer plus peptone. Above 10^4 cfu/g of soil, the plating efficiency of Tween C for Xcc-A and Xc was 92–100% of that of King's medium B and Difco nutrient agar (8,13), and the plating efficiency of KCB medium was 90–100% of that of NGA. Below 10^4 cfu/g of soil, the efficiency of recovery for Tween C and KCB decreased to levels as low as 50%.

Presumptive colonies of *Xanthomonas* from leaves and soil were streaked on NGA and tested for pathogenicity with a modification of a detached leaf assay developed for *X. c.* pv. *pruni* on peach leaves (14). Fully expanded but still immature leaves of Swingle citrumelo seedlings were separated into leaflets and surface-sterilized in 70% ethanol for 1 min. The leaflets were then rinsed with sterile distilled water twice and placed on 1.5% water agar plates with the adaxial surface of the leaf exposed. The leaflets were punctured 10 times, and 10 μl of a bacterial suspension containing 10^8 cfu/ml (determined spectrophotometrically) was placed on each wound. The lesions were erumpent 10–14 days after inoculation with XC62 and flat or blister-like after inoculation with X4600RS.

In Beltsville in 1987, a circular plot of Swingle citrumelo seedlings was established. The seedlings were grown in the greenhouse to a height of 1 m, a stem diameter of 2–3 cm, and a canopy diameter of about 0.5 m. The Xc strain

used was F1 (Civerolo; J. W. Miller, DPI, X84-3048), and the Xcc-A strain was XC62. The bacteria were prepared and the plants spray-inoculated as described previously. Thirty-two plants were planted in Duffield silt loam (sand, 30%; silt, 53%; and clay, 17%; pH 6.0) with a spacing of 1.5 m, in a circle 15 m in diameter. Eleven plants inoculated with Xcc-A and 11 inoculated with Xc were located on the east and west sides of the circle, respectively, and were bordered by five uninoculated plants on both the north and the south ends. Screens of 75% shade cloth, 1.2 m in height, were located between the inoculated plants and the control plants to act as a windbreak and reduce the probability of cross-contamination.

Every 3 wk, plants and soil from at least five inoculated and five uninoculated treatments were sampled as described for the previous experiment with the following modification. Three symptomless leaves per plant were collected, one from the top, one from the middle, and one from the bottom of the canopy; the leaves were combined into one sample for washing in 30 ml of buffer.

Population dynamics and survival in soil after nursery eradication. Two nurseries of the same design as those in Frederick were established in Argentina. The plots were located on Yuqueri sand (sand, 96.1%; silt, 1.3%; and clay, 2.6%; pH 5.8). Seedlings, 20–30 cm in height, of sweet orange (*C. sinensis* (L.) Osb. cv. Pineapple) and grapefruit (cv. Duncan) were planted in late spring of 1985 (November). A focal plant was inoculated as described above with the rifampicin-resistant strain LTV5 of Xcc-A from Concordia and was introduced into each plot. By late summer of 1987, the disease proportion (number of infected plants per total number of plants) and disease incidence on leaves had increased to 0.97 and 52%, respectively, in the grapefruit nursery, and to 0.89 and 24% in the sweet orange nursery. The 35th seedling from the western edge of the plot was then sampled in alternate north-south rows. Three leaves with lesions and three symptomless leaves from each of these plants and soil under each of them were collected as previously described. Bulked leaf samples and 2-g soil samples were each washed in 20 ml of phosphate buffer plus peptone, and 0.1-ml aliquots of the wash solution were plated in duplicate on a Tween medium amended with rifampicin (100 mg/L). Colony counts were expressed as the logarithm of the number of colony-forming units per gram of leaf or soil. After the removal of all of the plants in each nursery in March, the same soil sites were resampled 4 and 21 days later.

Grapefruit plants were reestablished in the same spatial arrangement at a different location, 20 m away. Weekly sampling of epiphytic populations on

symptomless leaves and of soil populations began immediately thereafter and continued for 18 wk. Four leaves and four soil samples were collected from along each of four transects, in the northeast, southeast, southwest, and northwest directions. Samples from each transect were bulked and processed as described for the preeradication sampling.

The following environmental conditions were recorded: soil ψ (cbar) on the day of sampling, cumulative rainfall (mm), cumulative radiation (hr), and the mean of daily temperature and relative humidity for the 5- to 9-day period prior to each sampling. The regression and general linear models procedures of the Statistical Analysis System (SAS Institute, Cary, NC) were used to analyze the relationships between soil populations, leaf populations, and these environmental conditions.

RESULTS

Recovery from soil in nursery epidemics. In Frederick, rainfall was sparse during the summer of 1986 (26–69 mm/mo). Soil ψ was maintained within a range of −5 to −10 cbar with supplemental overhead irrigation (Table 1).

Xanthomonads were consistently recovered from leaves affected with citrus canker from at least one of three groups of Swingle citrumelo seedlings each month from July to October (Table 1). Bacteria were not detected in samples from asymptomatic leaves of Flying Dragon trifoliate orange located in the rows adjacent to the line source of inoculum, and no symptoms of citrus canker appeared in these trees during the sampling period. Xanthomonads were recovered from soil under at least one group of diseased plants on each of the sampling dates except 9 September. In general, soil populations (per gram of soil) were lower than those associated with diseased leaves (per square centimeter). All strains isolated from leaves and soil that were tested for pathogenicity caused lesions on Swingle citrumelo in the detached leaf assay. The lesions were erumpent, which is characteristic of citrus canker.

Populations of Xc from leaves with symptoms of citrus bacterial spot were encountered less often and were 10–100 times lower than those from leaves with citrus canker. The rifampicin- and streptomycin-resistant Xc strain was recovered from soil only on 6 October, when populations exceeded 10^4 cfu/g of soil. The xanthomonads isolated from leaves and soil caused typical symptoms of citrus bacterial spot on detached leaves. No xanthomonads were recovered from Swingle citrumelo in the rows adjacent to the infected plants on any of the sampling dates, and no disease symptoms were observed in these rows.

In Beltsville in 1987, overhead irrigation was used as needed. Periodic

rainfall occurred through early July (38–100 mm per rain event), but none occurred between 13 July and 5 August. This was reflected by a drop in soil ψ from the sampling on 22 June to the sampling on 8 August (Table 2).

The number of positive detections on asymptomatic leaves sampled from diseased Swingle citrumelo was much higher in May and June than in July and August, when little rainfall occurred (Table 2). When populations of Xcc-A and Xc were detected on symptomless leaves of diseased plants, they were 10^3–10^4 cfu/cm^2 of leaf area. Compared to bacterial recoveries in Frederick, this population range was similar to that on leaves with citrus bacterial spot but was less than that on leaves with citrus canker. No xanthomonads were detected on uninoculated border plants.

Soil populations of Xc were detected in May and June, when the soil ψ was similar to that in Frederick in 1986, but were not detected in July and August, when the soil was drier. Although populations of Xcc-A on asymptomatic leaves were comparable to those of Xc, Xcc-A was not recovered from soil on any of the sampling dates. Bacteria in soil were detected in the area surrounding the

same plants from which bacteria were recovered from symptomless leaves. The populations of bacteria per gram of soil were approximately equal to or less than those per square centimeter of asymptomatic leaves.

Population dynamics and survival in soil after nursery eradication. In the grapefruit and sweet orange nurseries in Argentina, the proportion of diseased plants and the incidence of disease on plants after 15 mo of disease progress were greater than in the nursery plots in Frederick and Beltsville (the disease incidence was 24–52% in Argentina and less than 20% in Maryland). Populations of Xcc-A on severely diseased leaves of grapefruit and sweet orange exceeded 10^7 cfu/g of leaf (Table 3), compared to about 10^5 cfu/g of leaf infected with citrus canker in Frederick (Table 1). Lesioned leaves in the sweet orange and grapefruit nurseries had 10^2 and 10^3 times more bacteria than symptomless leaves, respectively. Xcc-A was not consistently detected on asymptomatic leaves. In soil, there were a greater number of detections than on symptomless leaves, but the populations were no greater (Table 3).

In the sweet orange plot, 4 and 21 days after the removal of the plants, no

Table 1. Recovery of a *Xanthomonas campestris* pv. *citri* strain (Xcc-A) and a nursery strain of *X. campestris* (Xc) from diseased leaves of Swingle citrumelo seedlings and the soil under the tree canopy in nursery epidemics of citrus canker and citrus bacterial spot in Frederick, Maryland, in 1986

| Date | Soil ψ (cbar) | Strain | Leaf population | | Soil population | |
			No. detected/ total observed	Log cfu/cm^2 of leaf[a]	No. detected/ total observed	Log cfu/g of soil[a]
24 July	−9	Xcc-A	3/3	5.71 ± 0.36	2/3	4.02 ± 0.29
		Xc	1/3	3.41	0/3	ND[b]
28 Aug.	−5	Xcc-A	2/3	5.37 ± 0.07	2/3	4.61 ± 0.65
		Xc	1/3	3.08	0/3	ND
9 Sept.	−10	Xcc-A	3/3	3.69 ± 0.21	0/3	ND
		Xc	0/3	ND	0/3	ND
6 Oct.	−6	Xcc-A	1/3	5.00	1/3	4.32
		Xc	1/3	4.17	1/3	4.11

[a] Mean of the positive detections plus or minus one standard deviation, for populations with more than one positive detection.
[b] Not detectable.

Table 2. Recovery of a *Xanthomonas campestris* pv. *citri* strain (Xcc-A) and a nursery strain of *X. campestris* (Xc) from symptomless leaves of diseased Swingle citrumelo trees and the soil under the tree canopy in epidemics of citrus canker and citrus bacterial spot in Beltsville, Maryland, in 1987

| Date | Soil ψ (cbar) | Strain | Leaf population | | Soil population | |
			No. detected/ total observed	Log cfu/cm^2 of leaf[a]	No. detected/ total observed	Log cfu/g of soil
30 May	−15	Xcc-A	2/6	4.01 ± 1.00	0/6	ND[b]
		Xc	3/6	3.12 ± 1.28	1/6	3.00
4 June	−20	Xcc-A	5/5	4.58 ± 0.90	0/5	ND
		Xc	4/5	4.31 ± 0.36	1/5	4.23
22 June	−30	Xcc-A	4/11	3.99 ± 1.39	0/11	ND
		Xc	2/11	3.16 ± 0.01	1/11	3.53
13 July	−100	Xcc-A	3/11	3.70 ± 1.01	0/11	ND
		Xc	2/11	3.54 ± 0.65	0/11	ND
8 Aug.	−1,000	Xcc-A	1/11	3.38	0/11	ND
		Xc	2/11	3.32 ± 0.01	0/11	ND

[a] Mean of the positive detections plus or minus one standard deviation, for populations with more than one positive detection.
[b] Not detectable.

bacteria could be detected in the soil at the previously sampled locations. In the grapefruit plot, Xcc-A was recovered as a single colony in one sample after 4 days, but a subsequent assay after 21 days was negative. During this period, the soil ψ of the sandy soil in the plot varied between -15 and $-1,000$ cbar.

After transplant of the trees from the grapefruit nursery to another location in late March, the sampling of asymptomatic leaves and of the soil beneath continued for 18 wk (in the fall and winter). In early April (fall), after nursery establishment, soil populations were 10^3–10^4 times lower than leaf populations and remained

lower throughout the entire sampling period (Fig. 1). In April, periodic rains occurred, and soil populations increased to 10^4 cfu/g of soil, whereas leaf populations remained at about 10^5 cfu/g of leaf. During May, the decrease and increase in both leaf and soil populations coincided with dry and wet periods, respectively. From June through August (winter), soil populations were 10–10^3 times lower than leaf populations. Fluctuations in Xcc-A populations on leaves and in soil during the winter did not coincide with periods of rainfall but occurred primarily in response to temperature.

When leaf populations and environmental factors were utilized in a regression model, all the parameters together explained 40% of the variation in soil populations. A model including rainfall, soil ψ, and temperature as well as leaf populations gave an R^2 of 0.37 ($n = 64$). The R^2 was slightly improved if the interaction between leaf populations and temperature was considered instead of the individual parameters. Soil and leaf populations were both significantly correlated with temperature ($r = 0.24$ and $r = 0.38$, respectively), but leaf populations were affected more by low temperature; hence, the interaction was

Table 3. Recovery of *Xanthomonas campestris* pv. *citri* from lesioned and symptomless leaves and from soil under the tree canopy in grapefruit and sweet orange nursery epidemics of citrus canker before and after plant removal (eradication) in Concordia, Entre Rios, Argentina, in March 1987

| Nursery | Lesioned leaves | | Symptomless leaves | | Soil before eradication | | Soil after eradication[b] |
	No. detected/ total observed	Log cfu/g of leaf[a]	No. detected/ total observed	Log cfu/g of leaf[a]	No. detected/ total observed	Log cfu/g of soil[a]	No. detected/ total observed
Grapefruit[c]	5/5	7.28 ± 0.42	2/5	3.89 ± 0.57	4/5	3.93 ± 1.13	0/5
Sweet orange[d]	5/5	7.89 ± 0.36	1/5	5.01	2/5	3.14 ± 0.21	0/5

[a] Mean of the positive detections plus or minus one standard deviation, for populations with more than one positive detection.
[b] Grapefruit and sweet orange nursery sites were sampled 21 days after eradication of the plants.
[c] Before eradication, the grapefruit nursery had a disease proportion of 0.97 and a disease incidence of 52%.
[d] Before eradication, the sweet orange nursery had a disease proportion of 0.89 and a disease incidence of 24%.
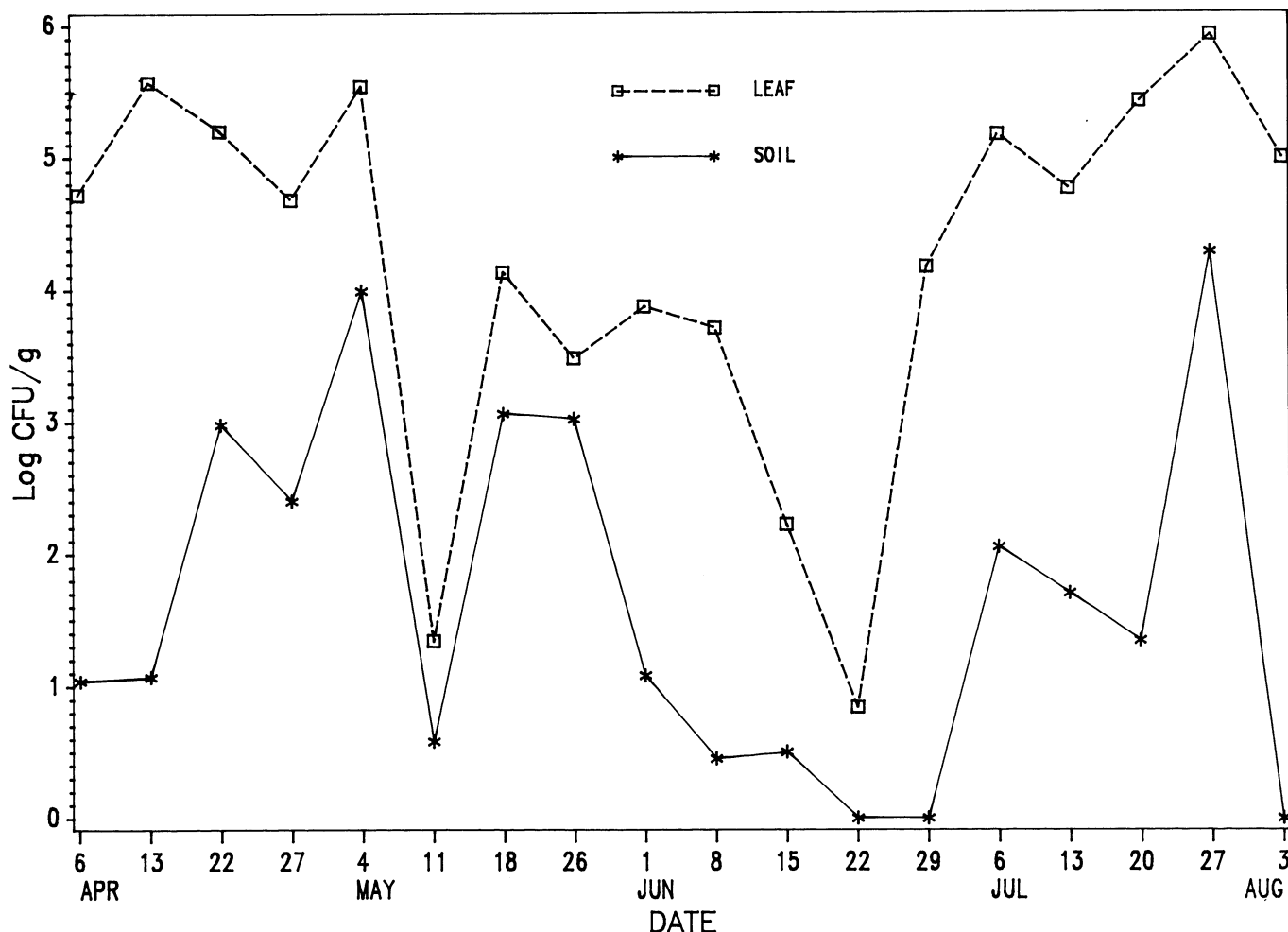
Fig. 1. Population dynamics of *Xanthomonas campestris* pv. *citri* from symptomless leaves and from soil under the tree canopy in a grapefruit nursery with a disease proportion of 0.97 in Concordia, Entre Rios, Argentina, from April to August 1987 (fall and winter).

significant. The model for predicting soil populations (SP) ($R^2 = 0.374$) was SP = 0.895 + 0.0000170(cB) + 0.108(RN) + 0.0153(LP * TP), where cB is soil ψ (cbar), RN is cumulative rainfall (mm), and LP * TP is the interaction of leaf populations and mean daily temperature for the 5- to 9-day period prior to each sampling. The partial R^2 for cB, LP * TP, and RN were 0.234, 0.190, and 0.168, respectively.

DISCUSSION

A question frequently raised after plant eradication in Florida citrus orchards and nurseries is whether the bacterial pathogens associated with citrus canker and citrus bacterial spot survive saprophytically in soil until the area is replanted with citrus. In Argentina, the bacterium was present in soil in grapefruit and sweet orange nurseries where a very high proportion of the trees were infested with citrus canker. After plant removal, Xcc-A was incapable of survival in sandy soil under subtropical conditions similar to those in Florida. In a previous study (8), there were few recoveries of Xc from soils in Florida nurseries before and after eradication. Furthermore, in Florida, Xc was not detected in soil under lightly diseased plants (with disease incidence less than 10%) in a Swingle citrumelo nursery after repeated sampling throughout the summer of 1987 (Graham and Gottwald, *unpublished*). These observations, taken together with a recent report from Brazil that Xcc-A survived no more than 35 days in a naturally infested sandy soil (12), support the conclusion that these bacteria have very limited survival capability under subtropical conditions. This may be due to the high temperatures and large fluctuations of water potential that occur in sandy soils between irrigations or rainfall events. In Argentina, temperature, rainfall, and soil ψ together explained a substantial amount of the variation in soil populations. The prolonged survival in fall and winter previously reported in Japan (3,4) presumably occurred under cooler and wetter conditions than in our studies.

Both Xcc-A and Xc were consistently recovered from soil in the presence of a heavily infected host (with disease incidence greater than 20%) under nursery conditions. There was no evidence of bacterial spread in soil, as bacteria were not recovered under adjacent uninfested plants. The population dynamics in soil appeared to depend on the movement of bacteria from infected leaves and stems into soil. Populations in soil were sometimes comparable to those on symptomless leaves on the tree but did not exceed those recovered from lesioned leaves. This indicates a dilution of bacteria as they were moved by irrigation, dew, or rainwater from lesions to symptomless tissue and soil. Without replenishment by bacteria from the canopy, populations in soil rapidly declined to undetectable levels. This was evident after nursery eradication when soil dried and populations did not recover when the soil was rewetted. A decline in soil populations also occurred in May, when unfavorable moisture conditions led to a rapid decline in epiphytic populations (e.g., Fig. 1). Thus, there was no indication of a saprophytic capability of *Xanthomonas* in the sandy soils studied.

Our observations in the field are confirmed by greenhouse and field studies in which the soil was artificially infested with Xcc-A (1,4,11). The bacterium is incapable of surviving in nonsterile, moist soils, in which it apparently is a poor competitor with other soil microorganisms (1,4,11). The ability to survive in artificially infested dry soil (1,4,11) appears to have little relevance to field situations. In Beltsville and Argentina, the lack of recovery where soil ψ was low (less than −100 cbar) indicates that the bacterium does not survive under dry soil conditions. This is in contrast to the prolonged survival of Xcc-A, Xc, and other xanthomonads in crop residues (8,10,15,17). Apparently, if the bacterium is protected in host tissue from rapid desiccation, it may survive for several months in a dry condition on the soil surface (8,17). Yet, conditions that favor decomposition of leaf material, such as burial in moist soil, lead to a more rapid decline in the population, probably due to competition with saprophytic soil microbes (8,10,15,17).

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