Bacterial Speck of Tomato: Sources of Inoculum and Establishment of a Resident Population

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ABSTRACT

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Bacteria capable of inciting speck on tomato leaves were isolated from roots and foliage of diverse weed and crop plants in soils with and without a history of tomato culture. In greenhouse and field experiments, soil-borne inoculum incited foliar symptoms of the disease. Also, *Pseudomonas tomato* (*P. syringae*) was isolated from apparently symptomless leaves collected from commercial tomato fields. Resident populations of the bacterium persisted for long periods in association with tomato leaves, but were reduced to low levels at 32 C even when free moisture was maintained for 48 hr. A portion of the resident population survived under warm, dry conditions in the field for at least 14 days after inoculation, but did not cause obvious symptoms. However, after leaves were wet for 24 hr, symptoms developed within 3-5 days. Exposure of tomato seedlings to 39 C for 6 hr before inoculation increased susceptibility to invasion and/or infection by the bacterium.

Additional key words: epidemiology, *Lycopersicon esculentum*.

In recent years, bacterial speck of tomato [which is caused by *Pseudomonas tomato (P. syringae)*] has become a serious problem on processing tomatoes (*Lycopersicon esculentum* Mill.) in many of California's production areas. Although the disease may occur at any time during the growing season, it is most severe in early spring plantings that are exposed to cool, moist conditions. Early infections may result in considerable economic losses (15).

Sources of inoculum for these sporadic epidemics have not been identified. We have attempted to demonstrate seed transmission in suspected commercial seed lots, but more than 20 tests conducted under conditions of temperature and moisture favorable for disease development did not demonstrate presence of the speck organism on seed (Schneider, *unpublished*). Furthermore, the disease has occurred in some fields planted to tomatoes for the first time. These observations suggested that the bacterium is ubiquitous and possibly is soil-borne. It also may have a resident phase as postulated and demonstrated by Leben (10, 11, 12) and others (4, 6, 20) for other bacterial plant pathogens.

This study was conducted to determine: (i) sources of inoculum of the speck organism, (ii) whether it is soil-borne, and (iii) the effects of temperature and moisture on survival of the resident population. Also, the significance of soil-borne and resident phases was assessed with respect to the epidemic development of the disease.

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MATERIALS AND METHODS

Field survey.—A survey was conducted during the spring of 1975 for the presence of the bacterial speck organism in agricultural and nonagricultural soils. Weeds and crop plants, including rhizosphere soil, were collected, placed in plastic bags, and stored over ice for transport to the laboratory. The next day stems and leaves were separated from roots with adhering soil. The plant parts were placed in flasks containing sterile distilled water and shaken for 30 min. The wash water was diluted in a $\log_{10}$ series with sterile distilled water, and 0.1-ml portions were spread on the surface of King's Medium B agar plates (9). After 48 hr, plates were examined under near-ultraviolet (UV) light and fluorescent colonies were marked for further tests. All marked colonies were tested for cytochrome oxidase reaction (17), and all oxidase-negative isolates were subcultured on medium-B slants and tested for pathogenicity in the greenhouse. Since most leaf-blighting pseudomonads are oxidase-negative (13), this procedure reduced the requisite number of pathogenicity tests.

Inocula for pathogenicity tests were prepared by washing 48-hr medium-B agar slant cultures with sterile distilled water; cell numbers were estimated from absorbance readings made with a spectrophotometer and final concentrations were adjusted to about 10^7 cells/ml by dilution with sterile distilled water. Sterile cotton swabs were dipped into the suspension and stroked gently across the upper and lower surfaces of the youngest fully expanded leaves of two 5-wk-old tomato plants (cultivar VF 145-B-7879). Sterile distilled water was applied in a

similar manner to noninoculated control plants. Plants were incubated on an open greenhouse bench (20-25 C). Pathogenicity tests were recorded positive when discrete black leaf spots surrounded by yellow halos were evident. Symptoms generally developed within 4 days, but final observations were made after 1 wk.

Effect of temperature and moisture on bacterial populations.—A culture of *P. tomato* (P107), recently isolated from infected tomato foliage, was maintained on medium-B agar slants at 4 C. Inoculum was prepared by washing cells from 48-hr-old cultures on yeast-dextrose-carbonate agar (19) slants with sterile distilled water. Suspended cells were centrifuged for 10 min at 1,500 *g*, resuspended in sterile distilled water, and adjusted to a concentration of about 10^4 cells/ml.

Tomato plants, grown in U.C. soil mix (1) (one plant per 15-cm diameter pot) in a greenhouse maintained at 20-25 C, were inoculated 8 wk after sowing by atomizing the bacterial suspension with a glass chromatography sprayer onto the upper and lower leaf surfaces until visible drops were apparent. This procedure deposited about 0.0013 ml inoculum/cm^2 of leaf area as determined by weighing leaflets of known area before and after inoculation. The atomizer nozzle was held in a horizontal position above the leaves so that the inoculum droplets settled gently onto the leaf surfaces. Thus, leaves were not watersoaked during inoculation. Plants then were allowed to dry for 2 hr at 26 C and 5% relative humidity (RH).

After drying, five plants were placed in each of three growth chambers maintained at a constant 17, 25, and 32 C with continuous light (4,800 lux) provided by fluorescent and incandescent bulbs. Each growth chamber was equipped with humidity controls and a misting device (DeVilbiss Model 272). Treatments consisted of allowing the plants to remain dry or under mist to maintain free water on the leaf surfaces for 6, 24, or 48 hr. After misting, the RH at all temperatures was maintained at 40-60%. Noninoculated control plants were included in each misting treatment.

Populations of *P. tomato* were determined immediately after the inoculated plants had dried, after the 6-, 12-, 24-, and 48-hr misting periods, and at 24-hr intervals thereafter. Five leaflets from the three youngest fully-expanded leaves, from each of the five plants in each growth chamber were taken at each sampling period. Two 1.2-cm diameter disks (cut with a No. 6 cork borer) were removed from each leaflet. Thus, a sample from each plant comprised 10 leaf disks which were combined. Leaf disks were homogenized for 20 sec in 20 ml of sterile distilled water in a 25-ml-capacity blender. The homogenate was diluted in a 10-fold series and 0.1 ml of each dilution was spread on the surface of a semiselective medium for pseudomonads (8) which had a plating efficiency of 43% as compared to medium-B for the isolate of *P. tomato* used in this study. After incubation for 5 days at room temperature (21 C), colony counts were made in plates which had less than 400 colonies per plate. Data on bacterial populations are presented as a percentage of those detected at zero time (just after the leaves had dried following inoculation). Initial counts ranged from 85 to 315 colony-forming units per square

TABLE 1. Association of *Pseudomonas tomato*, the causal agent of bacterial speck of tomato, with roots and leaves of various plants[a] collected from fields with or without history of tomato culture. Samples from 10 collection sites that did not yield pathogenic isolates were not included

Associated plant and common name	Collection site	Previous cropping history	Plant part	Number of isolates tested[b]		
				Fluorescent-	neg.	Path.
Lycopersicon esculentum Mill. tomato	Santa Clara County	3 yr in tomato with bacterial speck	leaves	54	4	0
			roots	61	20	5
Triticum vulgare L. wheat	Solano County	Previous year in tomatoes with bacterial speck	leaves	18	0	-
			roots	35	8	1
Beta vulgaris L. sugar beets	San Benito County	First year in cultivation, previously in rangeland	leaves	18	18	0
			roots	35	8	1
Brassica campestris L. wild turnip	Santa Clara County	Creek bed in >40-year-old prune orchard	leaves	23	5	1
			roots	80	19	3
Brassica nigra (L.) Koch black mustard	Santa Clara County	Creek bed in >40-year-old prune orchard	leaves	28	1	1
			roots	115	5	0
Matricaria matricarioides (Less.) Porter pineapple weed	Solano County	Uncultivated rangeland	leaves	4	0	-
			roots	53	14	2
Erodium botrys (Cav.) Bertol. broadleaf filaree	Santa Clara County	>40-year-old prune orchard	leaves	37	18	0
			roots	82	9	2
Erodium cicutarium (L.) L'Her redstem filaree	Santa Clara County	>40-year-old prune orchard	leaves	31	7	1
			roots	20	5	1

[a]Five to 10 plants were collected at each site and combined for assay.
[b]Serial dilutions made from leaves and roots were plated on King's Medium B agar. Only fluorescent colonies were tested for cytochrome oxidase reaction and only the oxidase-negative isolates were tested for pathogenicity (Path.) on tomato.

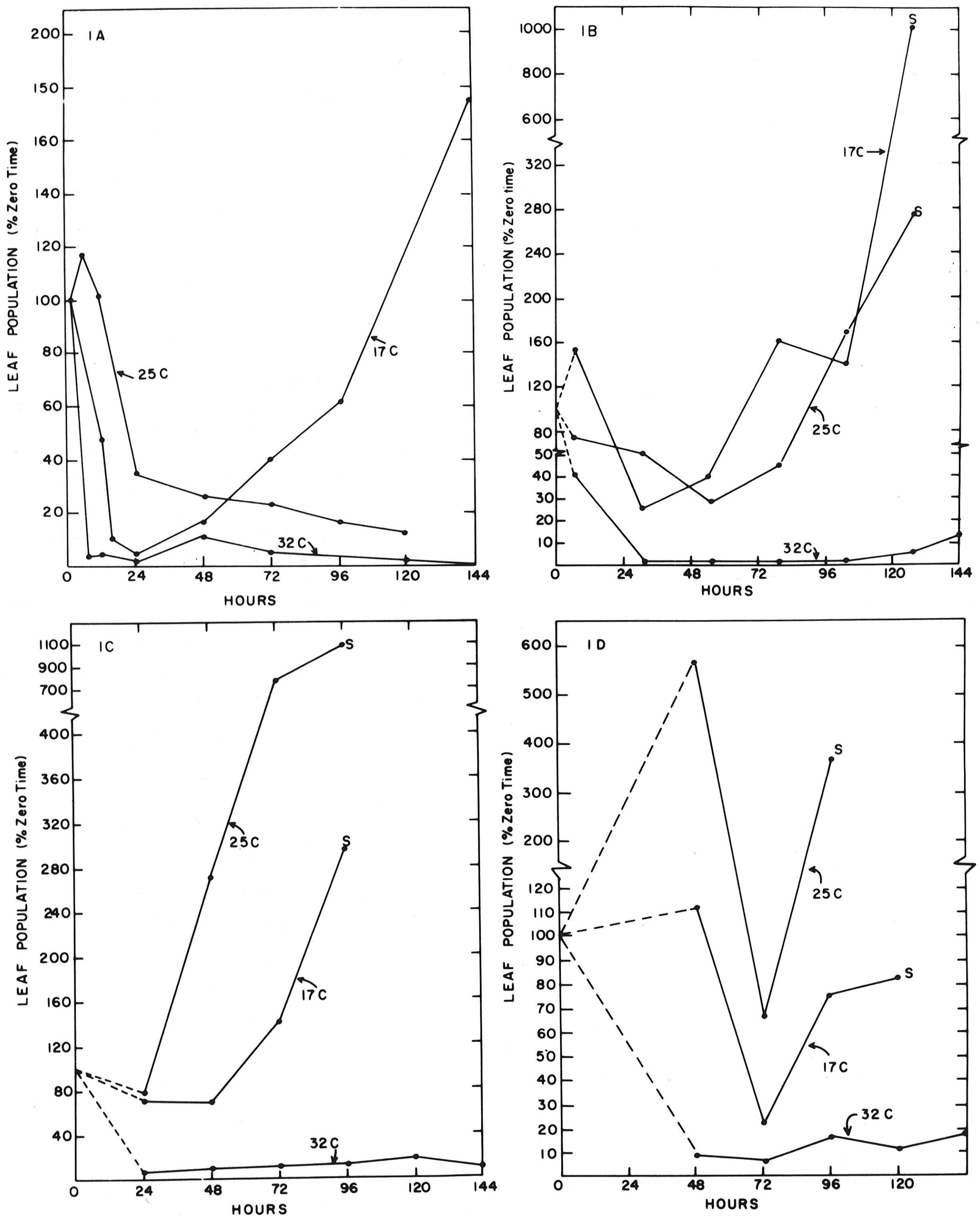

Fig. 1-(A-D). Effect of temperature and leaf wetness duration on resident populations of *Pseudomonas tomato* in association with tomato leaves. Inoculated and maintained **A)** dry, **B)** 6-hr mist, **C)** 24-hr mist, and **D)** 48-hr mist. Broken lines indicate duration of leaf wetness. Data are expressed as percent of population at zero time (population upon drying immediately after inoculation), which ranged from 85 to 315 colony-forming units per square centimeter of leaf area.

centimeter (CFU/cm^2) of leaf area. During the course of the experiment, 25 randomly selected colonies were subcultured and all were pathogenic on tomato following inoculations in the greenhouse.

Effectiveness of the resident population as inoculum after exposure to various temperatures at 40-60% relative humidity for 0-48 hr.—An experiment was conducted to determine the effectiveness of the resident population as a source of inoculum after exposure for different times to various temperatures. Plants were inoculated and allowed to dry as previously described. Treatments consisted of exposing groups of five plants to 12, 18, 24, 30, 33, 36, and 39 C at 40-60% RH for 0, 3, 6, 12, 18, 24, and 48 hr. Immediately after exposure, the plants either were placed directly on an open greenhouse bench (19-24 C) or incubated in a mist chamber at 22 C for 12 hr prior to placement on the bench.

Also included were two groups of five plants that were inoculated and dried as previously described, but were not exposed to specific temperatures. These plants either were misted for 12 hr or placed directly in the greenhouse. Noninoculated controls also were included. Leaf lesions were counted 10 days after removal of the plants from the mist chamber.

Survival of the resident population in the field.—During the morning of 6 August 1974 a 100-m row of furrow-irrigated tomato plants in the first green-fruit stage of development was inoculated with a suspension (10^4 cells/ml) of *P. tomato* applied with a pressurized hand-held sprayer as a fine mist over the plant canopy. As in the growth-chamber experiments, this method of inoculation precluded water-soaking of tissues. Plants were sprayed until droplets were evident on all leaves. The high and low temperatures on the date of inoculation were 32 and 20 C, respectively, and the average high and low temperatures during the 2 wk following inoculation were 33 and 12 C, respectively. After the inoculum had dried, and at 1- or 2-day intervals thereafter, leaves were collected and sampled for populations of *P. tomato* as described previously. Immediately after sampling misting devices were installed over the sampled plants which were kept wet for a 24-hr period. One week after misting, plants were observed for foliar symptoms of bacterial speck. Control plants were not inoculated but were treated similarly otherwise. Of 25 colonies that were subcultured and tested for pathogenicity during the course of the experiment, 22 were pathogenic. A total of 15 fluorescent bacterial colonies, none of which was pathogenic, grew on the assay plates from the noninoculated control plants.

RESULTS

Field survey.—The bacterial speck organism was found in association with various crop and weed plants growing in soils either previously cropped or not cropped with tomatoes (Table 1). There were no apparent symptoms on the leaves or roots of any of the plants from which the speck pathogen was isolated. Of a total of 1,502 fluorescent colonies from 20 samples, 254 were oxidase-negative. Seventeen of the oxidase-negative isolates produced typical bacterial-speck symptoms on tomato in greenhouse inoculations. There was no consistent ratio of oxidase-negative to -positive colonies in different samples, nor was there any consistency of association with different plant genera. Occasionally all of the fluorescent colonies from leaves or roots in a sample were either oxidase-negative or -positive. In most cases, fluorescent pseudomonads were the predominant bacterial microflora isolated on medium-B from both leaves and roots.

The frequent isolation of *P. tomato* from roots and adhering soil suggested that the bacterial speck organism is soilborne. A test was conducted in the greenhouse to determine if soil-borne inoculum could move to the leaves and incite disease. Infected tomato leaves were dried, ground to pass through a 0.25-mm (60-mesh) screen, and incorporated into pasteurized U.C. soil mix (0.5 g dried leaves/kg of soil). Noninoculated controls were treated similarly with material prepared from healthy leaves. The soils were placed in 15-cm diameter pots and tomato seeds were planted therein (10 seeds per pot). The pots were

TABLE 2. Average number of bacterial speck lesions produced per 6-wk-old tomato plant following inoculation and exposure for 3-48 hr to various temperatures at 40-60% relative humidity. Plants either were incubated in a mist chamber for 12 hr (M) or placed directly on an open greenhouse bench (D) immediately after removal from the various time/temperature treatments

Hours of exposure	Temperature (C)														LSD[b]	
	12		18		24		30		33		36		39			
	M	D	M	D	M	D	M	D	M	D	M	D	M	D	M	D
	Number of lesions per plant[a]															
3	51.1	3.0	47.2	3.9	63.4	3.2	54.0	1.7	57.0	2.4	45.6	1.8	58.0	0.7	8.9	1.8
5	52.3	3.5	57.7	3.7	71.8	2.8	63.2	0.6	54.4	0.2	34.4	0	99.2	0	11.2	0.9
12	50.0	4.3	61.8	4.0	86.8	2.8	50.8	0.2	40.2	0	29.8	0.4	40.8	0	10.4	1.1
18	47.3	4.8	67.6	2.7	88.4	3.0	50.6	0	43.2	0.4	29.6	0	23.2	0	8.7	1.7
24	45.4	4.1	51.2	3.4	86.8	2.1	45.2	0	33.8	0	26.8	0	2.5	0.2	9.2	1.9
48	39.3	2.7	56.4	4.0	109.0	1.6	40.6	0	26.4	0	17.6	0	3.2	0	10.0	2.2
LSD	[b]7.3	2.1	8.3	2.5	7.1	1.9	6.8	1.5	6.2	1.6	7.7	1.7	5.6	1.3		

[a]Lesion counts were made 10 days after the various treatments. There were 65.4 and 4.0 lesions per plant, respectively, on plants which were inoculated and either incubated in a mist chamber for 12 hr or placed directly on an open greenhouse bench.

[b]Least significant difference ($P = 0.05$).

incubated in a mist chamber for 1 hr each day until the first true leaves had emerged. At this time bacterial speck symptoms were apparent on the leaves of plants grown in the contaminated soil but not the control soil. Similar results were obtained in the field by transplanting healthy greenhouse-grown plants to an isolated section of a commercial tomato field that had a previous-year history of bacterial speck. The plants were sprinkler-irrigated for 2 hr each day for 3 wk, at which time typical speck symptoms were evident. No symptoms developed on another group of plants from the same seed lot which were grown under intermittent mist in pasteurized soil in a greenhouse.

Effect of temperature and duration of leaf wetness on resident bacterial populations.—The resident population on plants which were kept dry after inoculation declined to less than 40% of that at zero time within 24 hr at all temperatures (Fig. 1-A). At 25 and 32 C, the population remained at stable low levels for the duration of the experiment, but at 17 C the population gradually increased until the first symptoms were apparent after 144 hr. However, only eight leaf spots developed on all five plants. The populations followed the same general trend with 6 hr of leaf wetness, except that infection occurred at both 17 and 25 C and the populations increased at about the same rate until symptoms were evident after 120 hr (Fig. 1-B). After 24 hr of leaf wetness, the population at 17 and 25 C did not decline after misting was stopped; instead, there was an increase until symptoms developed after 96 hr (Fig. 1-C). As in the dry and 6-hr mist treatments, the population at 32 C declined to a very low level even during the period of leaf wetness, and symptoms were not evident after 96 hr.

Results were quite different with 48 hr of leaf wetness (Fig. 1-D). The population at 25 C increased to almost 600% of that at zero time during the wet period but fell off drastically upon drying. The population at 17 C increased only slightly while the leaves were wet and also decreased sharply after the leaves dried. Symptoms appeared within 72 and 96 hr at 25 and 17 C, respectively. Again, the 32-C population declined during the wet period and remained at a low stable level, and no symptoms were evident after 96 hr.

Effectiveness of the resident population as a source of inoculum after exposure to various temperatures at 40-60% relative humidity for 0-48 hours.—There was an inverse relationship between time of exposure of inoculated plants to 33, 36, and 39 C and the number of lesions per plant that developed within 10 days after misting for 12 hr (Table 2). Increasing the time of exposure of plants which were not misted to temperatures of 24 C and above resulted in fewer lesions per plant; exposures of 6 hr or more to 33 C and above almost completely eliminated the resident population. There was a statistically significant increase in the number of lesions on misted plants exposed to 39 C for 6 hr compared to plants exposed for 3 or 12 hr or more at 39 C. No symptoms developed on noninoculated, misted, or dry controls.

Previous studies indicated that temperatures above 32 C inhibited growth of the bacterium in vitro (R. W. Schneider, *unpublished*). Therefore, an experiment was conducted to determine if enhanced symptom development following the 6-hr exposure to 39 C was a result of increased susceptibility of the host. Ten plants were first exposed to 39 or 24 C for 6 hr, then inoculated and incubated in the mist chamber for 12 hr before placement on an open greenhouse bench. The lesions per plant, which averaged 112 and 71 in the 39- and 24-C treatments, respectively, were significantly different ($P = 0.05$).

Survival of resident populations in the field.—Resident populations of *P. tomato* in the field were maintained at a stable low level similar to the 32-C treatments in the growth chambers (Fig. 2). Immediately after inoculated leaves had dried, the population of fluorescent pseudomonads was 2.5 CFU/cm^2. At 1 day after inoculation, the population was less than 0.5 CFU/cm^2; by the third day, however, had increased slightly and thereafter (14 days) remained at about 4.3-6.0 CFU/cm^2. Populations of fluorescent pseudomonads on the noninoculated controls occasionally reached 0.1 CFU/cm^2 but isolates from these plants were not pathogenic.

Bacterial speck symptoms developed within 3-5 days following exposure of the plants which harbored these low resident populations to 24 hr of mist. This occurred when the mist was imposed after periods of up to 14 days following inoculation. No symptoms were evident on water-sprayed controls or on noninoculated plants which were exposed to the mist.

Results from the field experiment prompted a survey of commercial tomato fields from which leaves from apparently symptomless tomato plants were sampled for resident populations of the pathogen. These fields were in areas where the disease has occurred regularly for the past several years (Santa Clara Valley), but the survey was confined to fields in which bacterial speck was not evident at the time of sampling. Pathogenic isolates were recovered from leaves of symptomless plants selected at random in seven of 10 fields sampled. No pathogenic isolates were recovered from leaf samples taken from six fields in the warmer interior San Joaquin Valley where the disease had not been observed during the same period of time.

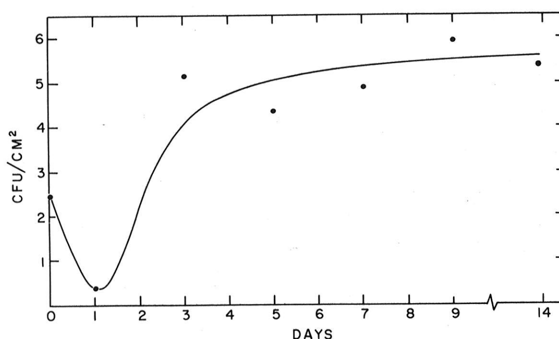

Fig. 2. Resident population of *Pseudomonas tomato* in association with leaves of field-grown tomato plants at days indicated after inoculation. Temperatures ranged from 12 to 33 C. Data are expressed as colony-forming units per square centimeter of leaf area.

DISCUSSION

Results from the soil surveys indicated that the

bacterial speck organism is ubiquitous, especially in the cooler coastal areas of California, and that it occurs in the rhizosphere of various plants growing in soils with no known history of tomato culture. We hesitate to identify all of the pathogenic isolates obtained as *P. tomato*, since the only characteristics which we determined were production of fluorescent pigment, a negative oxidase reaction, and pathogenicity on tomato. It is possible that some of the isolates that were pathogenic on tomato in greenhouse tests represent other nomenspecies which may not be capable of inciting speck of tomato under field conditions. Burki (2), for example, reported that *P. syringae*, *P. viridiflava*, and *P. fluorescens* were isolated from tomato leaf spots; however, the symptoms were not identical with those from which *P. tomato* was isolated. Our inoculation procedure for assessment of pathogenicity, in which leaves were not water-soaked or incubated in a mist chamber, should have prevented incorrect diagnoses in most cases. Several isolates were encountered which caused a hypersensitive response in tomato (discrete brown lesions), but these were not considered to be *P. tomato*.

The apparent ubiquity of the bacterial speck organism is similar to that reported for *P. syringae* (6) and *P. tabaci* (20). Valleau et al. (20) postulated that *P. tabaci* was primarily a rhizosphere inhabitant, and that the disease phase of its life cycle was only casual and not necessary for survival. Results of our greenhouse and field experiments support a similar conclusion for *P. tomato* and confirm that soil-borne inoculum is adequate for initiation of epidemics of bacterial speck.

Our results from growth chamber and field experiments indicated that *P. tomato* may exist as a resident, sensu Leben (11, 12), when unfavorable conditions for infection prevail. Thus, during periods of high temperature or in the absence of free moisture, the population declined, but was maintained at a low stable level. At temperatures below 32 C, the population increased after 6 and 24 hr of misting, but this probably resulted from bacteria that had initiated infection and multiplied during inoculation or misting rather than to an increase in the resident phase. These increases always were followed by the appearance of symptoms. The drastic decreases in the population upon drying following 48 hr of misting probably can be attributed to death of bacteria which had multiplied on the leaf surface during the prolonged misting.

The importance of free water in promoting growth of residents and subsequent infection is obvious from our results. We cannot preclude the possibility that sufficient moisture may have condensed on the leaf surfaces during small temperature fluctuations (± 1 C) to allow penetration and infection under relatively dry conditions at 17 C, but not 25 C. Even though RH was about the same at both temperatures, the vapor pressure deficits were quite different: 4.04 to 6.07 mm Hg at 17 C and 4.75 to 11.87 mm Hg at 25 C (16). Also, RH at the leaf surfaces at all temperatures was probably higher than ambient due to the boundary layer effect on transpiring leaves (3). Panopoulos and Schroth (14) demonstrated that several minutes of free moisture are sufficient to allow penetration of bean leaves by *P. phaseolicola*. Moreover, visible water congestion of leaf tissue is not essential for penetration and infection by bacteria (5, 14).

A portion of the applied inoculum was able to survive for up to 48 hr at temperatures ranging from 12 to 39 C. However, at 30 C and above, the surviving resident population was incapable of infecting without exposure to free moisture. At 12, 18, and 24 C there was no apparent change in infectivity of the resident population in plants which were not misted. However, the marked increase in lesions per plant with time of exposure to 24 C prior to misting may have resulted from multiplication of the resident population at or near infection courts; nevertheless, free moisture still was necessary for infection and symptom development.

Our field studies indicated that the resident phase can maintain itself at a stable level for at least 14 days of hot, dry weather. The appearance of symptoms within 3 or 4 days after wetting of the leaves confirmed the findings from growth chamber experiments indicating that the surviving inoculum is sufficient to initiate an epidemic. This has been demonstrated for several other bacterial plant pathogens (4, 7, 10, 18).

Results from our studies indicated that soil-borne *P. tomato*, which is ubiquitous and associated with many nonhost plants, can colonize tomato leaves and maintain itself as a resident under adverse environmental conditions for extended periods of time. When temperature and moisture are favorable, this resident population can then multiply and infect.

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