Epiphytic Survival of *Pseudomonas syringae* pv. *syringae* and *P. s. tomato* on Tomato Transplants in Southern Georgia

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ABSTRACT

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Pseudomonas syringae pv. *syringae* and *P. s. tomato* survived epiphytically on inoculated tomatoes grown for transplants in Tifton, Georgia, in April and May of 1988 and 1989. Populations of *P. s. tomato* declined faster as temperatures increased than did those of *P. s. syringae*. Populations of *P. s. syringae* were larger than those of *P. s. tomato* throughout the season. However, *P. s. syringae* was isolated most often in April, whereas *P. s. tomato* was recovered most often in May. The latter organism was isolated from inoculated plants before 1 May but was recovered from plants in commercial fields only once before 1 May. The two pathogens were never recovered from the same lesions, but epiphytic populations of *P. s. syringae* did not affect the epiphytic survival of *P. s. tomato* when both pathogens were sprayed on the same leaf.

Southern Georgia is a major production area for certified tomato (*Lycopersicon esculentum* Miller) transplants that are shipped to the northern United States and Canada. *Pseudomonas syringae* pv. *tomato* (Okabe) Young, Dye, and Wilkie, causal agent of bacterial speck of tomato, and *P. s. syringae* Van Hall, causal agent of syringae leaf spot of tomato, are often isolated from leaf spots surrounded with halos (4,8). Both diseases may occur in transplant fields, but only bacterial speck causes significant losses. Because infected or infested transplants may serve as the source of initial inoculum for fruit production fields, both production and transplant growers must adhere to recommended control measures such as the timely application of bactericides and purchase of only certified seed or transplants. However, part of the problem is bactericidal treatments can be used only as a preventive measure on clean plants. Once bacterial speck is diagnosed, all control measures become irrelevant and all transplants are lost, because transplant certification is based on a zero tolerance of disease. Hence, there is no reason to continue spraying transplants already diagnosed as having bacterial speck. This makes the use of certified transplants the only viable control practice.

Within the past 10 yr in the Georgia Department of Agriculture Plant Certification program, *P. s. syringae* and *P. s. tomato* have been recovered as pure cultures from lesions as well as from lesions that also contained *Xanthomonas campestris* pv. *vesicatoria* (Doidge) Dye or pectolytic xanthomonads (4,5). The two pseudomonads have never been recovered from the same lesion or from lesions on different plants in the same field. The purpose of this study was: 1) to conduct a survey in commercial fields to determine the incidence and distribution of *P. s. syringae* and *P. s. tomato* in 1988 and 1989 and 2) to compare the results to previous results from 1980–1984 (4) and 1985–1987 (Gitaitis, *unpublished*). In addition, we wanted to determine if *P. s. syringae* could establish epiphytic populations on tomato plants and whether those populations increased or decreased over time. Particular attention was paid to the survival of epiphytic populations of *P. s. tomato* on plants where epiphytic populations of *P. s. syringae* already had been established. We hoped that by studying the epiphytic populations of these two bacteria, their separate distributions in the field could be explained. In addition, if we found that populations of *P. s. syringae* suppressed populations of *P. s. tomato* in any way, we wanted to explore the potential use of *P. s. syringae* as a biocontrol agent.

MATERIALS AND METHODS

Commercial tomato transplant survey. During the 1988 and 1989 seasons, 10–20 lesions were sampled from each of 25 fields. Initially in 1988, single lesions were macerated in a drop of sterile distilled water and streaked onto both DL-lactate medium (4) and King's medium B agar (10) amended with 200 μg of cycloheximide L^{-1} (KMBC). Subsequently, 5-mm-diameter leaf disks, each containing a single lesion, were crushed in a tube containing 1 ml of sterile distilled water. After 15 min, the suspension was diluted serially (1:9) and spread onto KMBC (two plates per dilution) and DL-lactate medium (one plate per dilution). Plates were incubated at 27 C for 3 days and examined for fluorescent colonies. One fluorescent colony from each plate was characterized by the following tests: arginine dihydrolase (19), oxidase reaction (12), and utilization of erythritol, DL-lactate, and sucrose (6,15). One colony from each site was tested for hypersensitive reaction in tobacco (cv. K326) (11) and pathogenicity on tomato (cv. H-722).

Inoculum. Strain PSS 82-15S of *P. s. syringae*, originally isolated from lesions in tomato cv. New Yorker grown in Tift County in 1982, was naturally resistant to streptomycin and was ice-nucleation active. Strain PST 83-36 of *P. s. tomato* was isolated from tomato cv. H-2653 grown in Tift County in 1983.

A spontaneous mutant of strain PST 83-36 was obtained by streaking loopfuls of a turbid suspension (10^9–10^{10} cfu ml^{-1}) onto KMB plates amended with nalidixic acid (50 μg L^{-1}). The plates were incubated 4 days at 27 C. A single colony was selected and streaked onto the same medium. The procedure was repeated to obtain a pure culture. This strain was streaked onto plates of KMB amended with nalidixic acid at 100 μg/L (KMBN). A colony was selected and streaked onto a second plate of KMBN. The process was repeated, and the culture was stored as PST 83-36N. Cultures were maintained in vials of 15% sterile glycerol at −70 C and on KMB agar at 4 C.

Inocula for field tests were produced on KMB amended with 200 μg/L of cycloheximide (KMBC), KMBN, or KMB amended with 200 μg/L of cycloheximide and 100 μg/L of streptomycin (KMBCS). In a preliminary test, strain

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PST 83-36N failed to grow on media supplemented with cycloheximide and nalidixic acid. Therefore, cycloheximide was not incorporated into KMBN. Plates were incubated at 27 C for 48 hr. Bacterial cells were washed from the plates with distilled water and diluted to 50% transmittance at 600 nm, about 10^8 cfu/ml. Populations in the inocula were confirmed by spread-plate serial dilutions (1:9). Plates were poured with a Model MP-320 Pouramatic Automatic Petri Dish Filler (New Brunswick Scientific Company, Inc., Edison, NJ). Each plate contained 20 ml of medium. Pourite (Analytical Products Inc., Belmont, CA) was added to all media as an antifoam agent.

Experimental field plots. Field experiments were conducted in 1988 and 1989 at the Blackshank Farm of the Coastal Plain Experiment Station near Tifton, Georgia. Plots were established on a Tifton loamy sand soil at different locations each year. Rye (*Secale cereale* L.) was seeded as a cover crop, and strips of rye were maintained as windbreaks between plots. The cover crop was turned under with a moldboard plow, and the bed was harrowed. Napropamide (Devrinol) at 3.4 kg/ha, fenamiphos (Nemacur) at 8.99 kg/ha, and metalaxyl (Ridomil) at 2.34 L/ha were rototilled into the soil for control of weeds, nematodes, and damping-off, respectively. Fertilizer (6-12-6) at 343 kg/ha was broadcast and incorporated into the soil. A side-dressing (448 kg/ha) was applied 4 wk after planting. All plots were sprayed with carbaryl (Sevin 80%) at 2.2 kg/ha and chlorothalonil (Bravo 720) at 2.63 kg/ha on a 7-day schedule for insect and fungal leaf spot control, respectively. The plants were clipped on a 3- to 4-day schedule to promote uniform growth and to maintain a final plant height of 22.5 cm. Irrigation was applied as needed by solid-set overhead sprinklers. U.S. National Weather Service thermometers were used to measure maximum and minimum daily air temperatures.

Coated tomato seeds (cv. H-722) were direct-seeded 1 cm apart on 18 March 1988 in raised beds with four rows spaced 35 cm apart. There were three treatments—inoculation with *P. s. syringae*, inoculation with *P. s. tomato*, and a noninoculated control—and four replications arranged in a randomized complete block. Each plot was 6.1 m long and 5.2 m wide. A 0.61 × 5.2 m strip of plants in the center of each plot was inoculated on 13 April or 23 April.

In 1989, coated tomato seeds (cv. H-7135) were seeded on 20 February, 13 March, and 3 April as described above. There were four treatments—inoculation with *P. s. syringae*, inoculation with *P. s. tomato*, inoculation with *P. s. syringae* followed by inoculation with *P. s. tomato*, and a noninoculated control—and four replications arranged in a randomized complete block. Each plot was 15.9 m long and 5.2 m wide. A 6.9 × 5.2 m strip of plants in the center of each plot was inoculated with PSS 82-15S on 12 April, 21 April, and 4 May or with PST-N on 21 April, 29 April, and 11 May. Inoculum was prepared as described above and applied with a hand-pressurized sprayer (Model 2002, RL Corp., Lowell, MI) until runoff. All inoculations were made in the early evening hours (1800–2000).

Symptomless tomato leaflets were collected on two dates in 1988 and every 5–7 days (until 65 days after planting) in 1989 for each inoculation date to determine the epiphytic populations of *P. s. syringae* and *P. s. tomato* on tomato plants. Tomato leaflets were collected in the morning (0900-1000) and placed in plastic bags. Samples were collected with forceps that had been sterilized in 70% ethanol and air-dried. Tomato leaves, 1 and 3 g per replication, were placed in 250-ml flasks containing 20 and 75 ml of phosphate-buffered saline (PBS) supplemented with 1 g of chlorothalonil (Bravo 500) per liter of PBS in 1988 and 1989, respectively. Flasks were shaken on a rotary shaker at 200 rpm for 1 hr. Serial dilutions (1:9) were made, and 0.1-ml aliquots were spread onto the appropriate growth media. Colonies on KMBC were counted under ultraviolet light after 2 days of incubation at room temperature, and those on KMBCS and KMBN were counted after 3 days of incubation. Analysis of variance, general linear model analysis, and the Waller-Duncan (20) multiple range test were performed on raw and transformed data (log [n + 1]) (7). Isolations from lesions were made on KMBC as described above.

RESULTS

Commercial tomato transplant survey 1988–1989. *P. s. syringae* and *P. s. tomato* were isolated from 76 and 32%, respectively, of the commercial fields surveyed. In 1988, 83% of all syringae leaf spot diagnoses were made in April but the first diagnosis of bacterial speck was not made until 17 May. In 1989, 54% of all syringae leaf spot diagnoses were made in April and the first diagnosis of bacterial speck was made 26 April. On that date, *P. s. tomato* was recovered with *P. s. syringae* from plants from the same two fields but not from the same lesions. However, 75% of all bacterial speck diagnoses were made after 1 May and the disease was not found in association with syringae leaf spot. In a summary of data from records of the Georgia Department of Agriculture, *P. s. syringae* accounted for 88% of the diagnoses made from specklike lesions and was most prevalent in April during a 10-yr period (1980–1989) (Fig. 1). Furthermore, the number of isolations from which *P. s. syringae* was recovered dropped sharply during May, whereas the number of times *P. s. tomato* was recovered rose (Fig. 1).

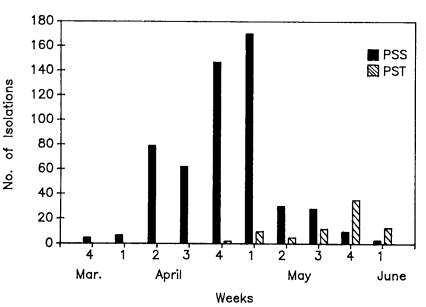

Fig. 1. A survey of syringae leaf spot, caused by *Pseudomonas syringae* pv. *syringae* (PSS), and bacterial speck, caused by *P. s. tomato* (PST), on tomato transplants in southern Georgia during a 10-yr period (1980–1989).

Symptoms of syringae leaf spot were observed most often in the lower part of the tomato canopy, whereas bacterial speck symptoms were distributed throughout all canopy heights. Typically, fewer syringae leaf spot lesions occurred per leaflet or per plant. Also, syringae leaf spot lesions usually were light brown without distinct halos, whereas bacterial speck symptoms were more striking in the field. Lesions were numerous and dark (brown or black) and frequently were accompanied by distinct halos in the later stage of development. The mean population of *P. s. tomato* from lesions from commercial tomato transplants was 8.1 × 10^6 cfu per 5-mm-diameter disk and was significantly greater ($P = 0.05$) than the mean populations of *P. s. syringae* (9.5 × 10^5 cfu per disk) recovered from lesions.

Experimental field plots. In 1988, epiphytic populations of *P. s. syringae* were similar at 9 and 25 days after either inoculation date (Table 1), but none of the plants developed lesions. Stable populations of *P. s. tomato* resulted from the first inoculation date (13 April), and plants developed typical bacterial speck lesions within 15 days. Initially, the mean air temperatures during this period of time were below or equal to the mean air temperatures of the preceding 8 yr

Table 1. Epiphytic populations of *Pseudomonas syringae* pv. *syringae* strain PSS 82-15S and *P. s. tomato* strain PST 83-36 on symptomless leaves of tomato transplants for two inoculation dates during 1988 near Tifton, Georgia

Strain	Inoculation date	Log cfu/g fresh weight after inoculation[y] 9 days	25 days
PSS 82-15S	13 April	5.0 a[z]	4.4 a
	23 April	3.2 a	2.3 a
PST 83-36	13 April	4.9 a	4.9 a
	23 April	7.3 a	1.2 b

[y] Mean of four replications.
[z] Means followed by the same letter within each row are not significantly different according to analysis of variance ($P = 0.05$).

(Fig. 2). In contrast, populations of *P. s. tomato* had significantly declined by 25 days after the second inoculation date (23 April). In general, the temperatures were below or near the mean air temperatures of the preceding 8 yr (Fig. 2). Bacteria recovered from the lesions were typical of *P. s. tomato*, e.g., they were fluorescent on KMB and negative for arginine dihydrolase and oxidase and for utilization of erythritol or DL-lactate.

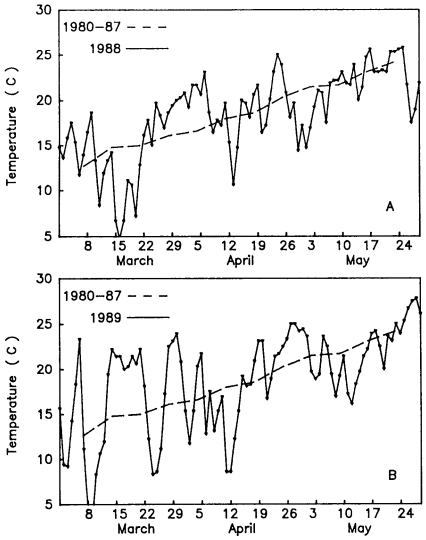

Fig. 2. Mean daily air temperatures (the sum of the daily maximum and minimum values divided by two) during the **(A)** 1988 and **(B)** 1989 tomato transplant seasons in southern Georgia compared with mean temperatures for 8 yr (1980–1987) for the same days and months of the season.

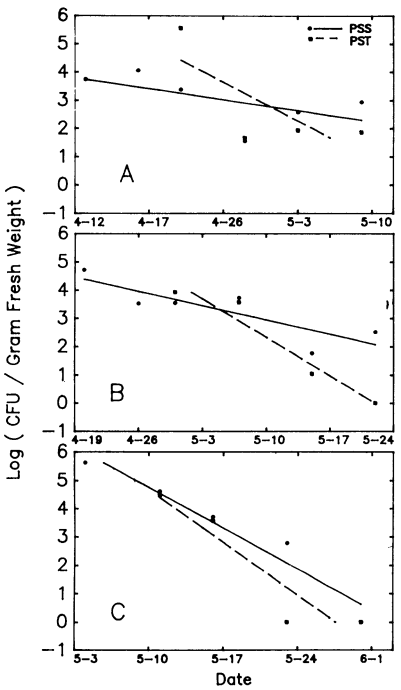

Fig. 3. Epiphytic survival of *Pseudomonas syringae* pv. *syringae* (strain PSS 82-15S) and *P. s. tomato* (strain PST 83-36N) on tomato transplants in southern Georgia in 1988. Points represent log cfu g^{-1} fresh weight of tomato leaflets after the following inoculation dates: **(A)** 12 April, **(B)** 21 April, and **(C)** 4 May for PSS 82-15S and **(A)** 21 April, **(B)** 29 April, and **(C)** 11 May for PST 83-36N. Regression equations and correlation coefficients are: **(A)** $y = 3.79 - 0.06x$, $r = 0.59$ for PSS and $y = 6.38 - 0.19x$, $r = 0.76$ for PST; **(B)** $y = 4.45 - 0.07x$, $r = 0.85$ for PSS and $y = 6.42 - 0.19\ x$, $r = 0.97$ for PST; and**(C)** $y = 6.19 - 0.21x$, $r = 0.97$ for PSS and $y = 6.51 - 0.27x$, $r = 0.93$ for PST.

In 1989, epiphytic populations of *P. s. syringae* and *P. s. tomato* were negatively correlated with sampling date after each inoculation date (Fig. 3). Declines in populations of *P. s. tomato* were significantly greater than declines in populations of *P. s. syringae* ($P = 0.05$) for each inoculation date. When the data from the three inoculation dates were combined and analyzed separately for each bacterium, populations of both pseudomonads tended to decline ($P = 0.1$) for the third inoculation date. Populations of *P. s. syringae* and *P. s. tomato* on the same plants over a 4–7 wk period were unaffected by the presence of each other when compared with populations on similar plants that harbored only one of the pathogens (Tables 2 and 3).

P. s. syringae was recovered only from lesions that developed after the first two inoculation dates. No lesions resulted from the third inoculation (4 May), although mean daily air temperatures throughout the expected incubation period were lower than the 8-yr mean for that time period (Fig. 2). Although most strains were resistant to streptomycin, wild types of *P. s. syringae* sensitive to the antibiotic also were isolated on KMBC. In contrast, *P. s. tomato* was isolated from lesions after all three inoculations and from all replications. However, the first isolation of *P. s. tomato* from a lesion was not made until 30 April. The mean air temperatures for the preceding 2 wk generally were higher than the 8-yr mean (Fig. 2). In addition, *P. s. tomato* was isolated from lesions on plants in plot areas that initially were inoculated with only *P. s. syringae*. All strains of *P. s. tomato* recovered from lesions were resistant to nalidixic acid, as was the original strain applied.

DISCUSSION

The separate disease outbreaks and distributions of populations of *P. s. syringae* and *P. s. tomato* in tomato transplants in southern Georgia over the last 10 yr appear to be primarily a function of time rather than antagonism between the two organisms. There was no evidence that populations of *P. s. syringae* adversely affected populations of *P. s. tomato*. Consequently, we concluded that there was little reason for studies on the use of *P. s. syringae* as a biocontrol agent for bacterial speck.

Regardless of the pathogen or the time of inoculation, epiphytic populations declined over time. In both 1988 and 1989, epiphytic populations of *P. s. tomato* declined faster than those of *P.*

Table 2. Epiphytic populations of *Pseudomonas syringae* pv. *syringae* strain PSS 82-15S on symptomless leaves of tomato transplants for three inoculation dates during 1989 near Tifton, Georgia[x]

Inoculation date	Strain	Log cfu/g fresh weight on sampling dates[y]					
		1	2	3	4	5	6
12 April	PSS	3.7 a[z]	4.1 a	3.4 a	1.6 a	2.6 a	3.0 a
	PSS-M	3.7 a	4.0 a	3.9 a	2.6 a	1.8 a	2.5 a
21 April	PSS	4.7 a	3.5 a	3.6 a	3.7 a	1.8 a	2.5 a
	PSS-M	4.9 a	3.5 a	3.5 a	4.3 a	1.8 a	1.9 a
4 May	PSS	5.7 a	4.6 a	3.7 b	2.8 a	0.0 a	NT
	PSS-M	5.6 a	4.3 a	4.4 a	2.8 a	0.0 a	NT

[x]Strain PSS 82-15S alone or followed about 1 wk later by inoculation with *P. s. tomato* strain PST 83-36N (PSS-M); PSS 82-15S was the strain monitored.
[y]Mean of four replications. Plants were sampled the day after inoculation and then weekly.
[z]For each sampling date, means of paired values with the same letter are not significantly different according to Waller-Duncan's multiple range test ($P = 0.05$). NT = not tested.

Table 3. Epiphytic populations of *Pseudomonas syringae* pv. *tomato* strain PST 83-36N on symptomless leaves of tomato transplants for three inoculation dates during 1989 near Tifton, Georgia[x]

Inoculation date	Strain	Log cfu/g fresh weight on sampling dates[y]			
		1	2	3	4
21 April	PST	5.6 a[z]	1.7 a	1.9 a	1.9 a
	PST-M	5.6 a	2.2 a	0.6 a	0.5 a
29 April	PST	3.9 a	3.6 a	1.0 a	0.0
	PST-M	3.4 a	2.9 a	1.0 a	0.0
11 May	PST	4.5 a	3.6 a	0.0	NT
	PST-M	4.4 a	3.5 a	0.0	NT

[x]Strain PST 83-36N alone or preceded about 1 wk by inoculation with *P. s. syringae* strain PSS 82-15S (PST-M); PST 83-36N was the strain monitored.
[y]Mean of four replications. Plants were sampled the day after inoculation and then weekly.
[z]For each sampling date, means of paired values with the same letter are not significantly different according to Waller-Duncan's multiple range test ($P = 0.05$). NT = not tested.

s. syringae. Higher temperatures may adversely affect epiphytic populations of *P. s. tomato* to a greater extent than those of *P. s. syringae*. Similar declines in populations of *P. s. tomato* have been attributed to high temperatures in previous reports (17,18). In Israel, the disease developed and spread only at temperatures between 13 and 28 C and at high relative humidity with free water on leaves (21). However, Gitaitis et al (4) observed bacterial speck symptoms on tomato transplants in southern Georgia only after 1 May, when daily high temperatures frequently exceeded 28 C. Results in this study were similar, as bacterial speck generally was not observed in commercial fields until after 1 May (the one exception occurred on 26 April 1989). This was the only recovery of *P. s. tomato* from commercial tomato transplants before 1 May in the last 10 yr. In that instance, both *P. s. syringae* and *P. s. tomato* were isolated from different lesions collected from plants in the same field. The mean daily air temperatures were higher than the 8-yr mean temperatures for that time of year. We do not understand why bacterial speck symptoms develop after epiphytic populations have begun to decline or why incidence is higher in May, but possible reasons include the source of inoculum and length of the incubation period. Under the climatological conditions of southern Georgia, weeds and plant debris were considered unlikely sources of inocula for bacterial speck, but seeds were considered the primary source of inoculum (14). Kim (9) reported that a 30-day period at 17–26 C is needed for the first appearance of symptoms in plants grown from naturally infested seed. Devash et al (3) found that 9–12 days were required for symptom expression in plants grown from artificially infested seed. Although the length of the incubation period depended on the inoculum concentration, it was not clear if they measured the number of days from planting or plant emergence. Conceivably, the incubation period in plants grown from infested seed plays a role in the temporal distribution observed for bacterial speck in southern transplants. We do not know if source of inoculum is a factor in the temporal distribution of these two diseases, but further research on the effects of inoculum density on incubation period and naturally vs. artificially infested seed appears warranted.

The ramifications of declining epiphytic populations are not fully known. Typically, transplants are shipped to northern areas where temperatures would be lower than in southern Georgia. Most strains of *P. s. syringae* recovered from tomato and pepper transplants are ice-nucleation active (1,4,8) and are a potential cause of frost damage if they are residents on transplants shipped north. Bonn and Gitaitis (1) reported similar results to ours in that epiphytic populations of *P. s. syringae* declined on pepper and tomato transplants whether the plants remained in Georgia or were transplanted in Canada. In contrast, Bonn et al (2) observed no decline in numbers of epiphytic *P. s. tomato* on tomato transplants shipped from Georgia to Canada, but they did not sample past 8 days after plants arrived in Canada and symptoms became apparent. Lindow et al (13) found that frost damage of corn seedlings was correlated with concentration of ice-nucleation active bacteria applied. Consequently, if epiphytic populations of *P. s. syringae* continue to decline on tomato foliage in Georgia before their shipment to cooler environments, the chances of plant damage by late spring frosts may be reduced. However, O'Brien and Lindow (16) reported that ice nucleation frequency varies in response to different factors, including host. They found that fewer ice-nucleation active bacteria were required to induce ice nuclei when grown on tomato leaves than when produced in vitro. Although rye was not included in their study, they found that corn and oats lowered the ice nucleation frequency of strains of *P. s. syringae* recovered from tomato, bean, and cucumber. Rye has been implicated as an epiphytic host for *P. s. syringae* (4) and is used in most transplant fields in Georgia as a cover crop and windbreak. It was not an objective of this study to determine if rye serves as an intermediate host for tomato strains of *P. s. syringae*, if either rye or tomato lowers the ice nucleation frequency in *P. s. syringae*, or if declining epiphytic populations of *P. s. syringae* on tomato will reduce frost damage once transplants are shipped north. However, future research in regard to population dynamics of ice-nucleation active bacteria on transplants and the effect on plants shipped north appears warranted.

Although there have been many previous instances where syringae leaf spot has resembled bacterial speck, during the 2-yr period of this study, only one commercial tomato transplant field contained plants that had syringae leaf spot symptoms likely to be confused with those of bacterial speck. Color, location, and number of lesions may be helpful for a tentative diagnosis but do not appear adequate for plant certification. We recommend that laboratory isolations and analyses be continued to ensure that certifications remain accurate.

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