Sources and Management of *Pseudomonas syringae* pv. *phaseolicola* and *Pseudomonas syringae* pv. *syringae* Epiphytes on Dry Beans in Colorado

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ABSTRACT

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Investigations during 1984 and 1985 demonstrated that *Pseudomonas syringae* pv. *phaseolicola* (Psp) and *Pseudomonas syringae* pv. *syringae* (Pss) occur as epiphytes on dry beans in Colorado. Populations of syringae-type pseudomonads (STPs) were detected on volunteer bean plants throughout northeastern Colorado. Commercial bean seedlings were free of STPs, suggesting that western-grown, certified seed lots had no, or relatively low, levels of STP contamination. Epiphyte population enumeration by replicate dilution plating was facilitated by a modification of Harris and Sommers dilution plate frequency method. Populations of STPs increased in experimental plots not sprayed with cupric hydroxide until early flowering. Bacterial populations in these plots decreased after spraying and then increased rapidly as plants matured. Pss dominated the STP epiphytic populations isolated from young plants in 1984, whereas Psp became predominant later in the season in 1984 and 1985. Cupric hydroxide foliar sprays significantly reduced or limited establishment of STPs on bean foliage. Determination of the effect of bactericides on epiphyte populations provides essential information needed to improve control strategies for halo blight and bacterial brown spot of dry beans.

Additional key words: ice nucleation activity, *Phaseolus vulgaris* L.

In 1959, Crosse (3) reported that the phytopathogenic bacterium *Pseudomonas syringae* pv. *morsprunorum* (Wormald) existed as an epiphyte on sour cherry (*Prunus cerasus* L. 'Montmorency') foliage and suggested this was an important inoculum source for subsequent canker development on stems and branches. Investigations into the epidemiology of other foliar bacterial diseases provided numerous examples of phytopathogenic bacteria with epiphytic phases on their hosts (9).

Pseudomonas syringae pv. *syringae* van Hall (Pss), the causal agent of bacterial brown spot, is a frequent foliar epiphyte on bean (*Phaseolus vulgaris* L.) (4,5). In Wisconsin, an epiphytic population of approximately 10^4 per gram of snap bean leaf tissue was the minimum apparent infection threshold required to produce bacterial brown spot symptoms (12). Numerous other plant species have been found with Pss epiphytes (13). Epiphytic contamination of hairy vetch (*Vicia villosa* Roth) with Pss was correlated with bacterial brown spot outbreaks in nearby snap bean fields (5).

Pseudomonas syringae pv. *phaseolicola* (Burkholder) Young et al (Psp), the causal agent of halo blight of bean, has not been reported as a naturally occurring epiphyte. However, a rifampin-resistant mutant of Psp was capable of establishing an epiphytic phase on bean leaves (23).

Outbreaks of halo blight and bacterial brown spot can seriously reduce yield and the quality of seeds and pods (15,18,21,26). Control of either bacterial disease by copper-based bactericides has been inconsistent (1,6,14,15,22,24,25). Some of this inconsistency may be caused by inappropriate timing of applications in relation to initial disease appearance, although other factors, such as varietal susceptibility and postapplication environmental conditions, are probably also involved. Bactericide applications could influence the epiphytic population dynamics of bacterial pathogens and ultimately their host-parasite relationships.

Our investigation was conducted to study the epiphytic association of Pss and Psp with dry bean foliage in northeastern Colorado and to evaluate the effect of a copper-based bactericide on their population dynamics.

MATERIALS AND METHODS

Sampling volunteer beans. During May and June in 1984 and 1985, commercial fields previously cropped to dry beans were scouted for the presence of volunteer bean plants with symptoms of halo blight and/or bacterial brown spot. Suspect lesions were cultured on King's medium B (KB) (10). Fluorescent pseudomonads, which were oxidase negative and possessed colony characteristics typical of syringae-type pseudomonads (STPs), i.e., blue green fluorescence, slow growth, flat rough-edged colonies, were reisolated and characterized. If lesions were not detected, 20–40 leaflets were collected, placed in a plastic bag, and stored on ice in a chest. Bulked leaf samples were later placed in a 500-ml Erlenmeyer flask containing 200 ml of sterile phosphate buffer (SPB) (16) and vigorously agitated on a horizontal shaker for approximately 30 min. The supernatant was diluted serially and plated on KB. After 3 days of incubation at 22 C, plates were examined for colonies typical of STPs.

In 1984, commercial bean fields in the proximity of volunteers associated with halo blight and bacterial brown spot were scouted for disease development during the growing season.

Seedling epiphyte survey. Emerging seedlings in commercial bean fields in northeastern Colorado were sampled for the presence of foliar epiphytic STPs during May and June in 1984 and 1985 (19 and 24 fields, respectively). Twenty to 40 unifoliate leaves were collected from random plants within each field, placed in a plastic bag, which was sealed, and stored either in an ice chest (1984 and 1985) or liquid nitrogen (1985). Loose soil was removed from leaves in the laboratory by gently blowing with compressed air or rinsing with distilled water. Leaves were processed in the same manner as those from volunteer plants. After incubation for 3 days at 22 C, plates were evaluated for STP colonies.

Copper efficacy study. In 1984, an experiment was conducted in two commercial dry bean fields near Holyoke in northeastern Colorado to evaluate the effect of two copper spray programs on foliar bacterial epiphytes. Sites A and B were located in an overhead sprinkler-irrigated pinto cultivar Olathe and a furrow-irrigated pinto cultivar U.I. 114 bean field, respectively. The experiment was repeated in 1985 in two furrow-irrigated pinto cultivar Olathe bean fields (sites C and D). In both years, the fields were planted during the first 3 wk of June and received only those foliar pesticide treatments described in this study. A randomized complete block design with four replicates and three treatments was used. The four-row plots (76-cm row spacing) were 15 m long, with a two-row untreated buffer between treatments and a 1.5-m buffer between blocks. Cupric hydroxide (copper equivalent 24.4%) was applied at 4.7 L of product in 234 L of water per hectare with a CO_2 powered backpack sprayer. Treatments were not applied to control plots. The bactericide was applied three times in an early program (3, 11, and 17 July 1984; 17, 24, and 31 July 1985), and twice in a late program (17 and 24 July 1984; 31 July and 6 August 1985). The spray applications were initiated when environmental conditions appeared conducive for halo blight and bacterial brown spot development and spread. Applications were timed on a 6- to 8-day schedule to provide continuous coverage during the treatment period.

Foliage samples were collected from both sites between 6:30 am and 8:30 am MST, on five dates each year (6, 19, and 26 July, 3 and 14 August 1984, 11, 18, 24, and 31 July, and 7 August 1985). The samples were processed within 12 hr of collection. In 1984, 20 symptomless, two-thirds to fully expanded trifoliate leaves were collected randomly from each plot, sealed in a resealable plastic bag, and placed on ice in a chest. A single random leaflet was detached from each trifoliate in the laboratory and bulked in a 500-ml Erlenmeyer flask with 200 ml of SPB. This buffer combines with copper residues, inhibiting their in vitro bactericidal activity (16). In 1985, 40 symptomless, individual leaflets were collected randomly and processed as in 1984. Flasks containing leaf samples were agitated vigorously for 20 min (1984) or 1 hr (1985) on a horizontal shaker to suspend epiphytic bacteria. The bacterial suspensions were diluted serially (six to nine 1:4 dilutions) in SPB, and replicate-plated onto KB plates by a modification of the Harris and Sommers plate frequency dilution method (7).

The following modifications facilitated dilution plate preparation and increased sample sets per plate. Autoclaved KB was cooled to 47 C in a water bath before pouring. After pouring, plates were dried at room temperature for at least 3 days. Bottoms of plates were marked for orientation and aligned on a template consisting of 24 1-cm-diameter circles (Fig. 1). An Eppendorf repeater pipette was used to dispense 10-μl aliquots of each dilution onto the plate above each circle. Three subsamples of eight spots were prepared for each dilution. Plating was performed in a laminar flow hood, where plates were left open for about 20 min to air dry before incubation. Plates were incubated at 22 C for 3 days and realigned for enumeration on the template. Total bacterial counts (one or more colonies) and fluorescent pseudomonads possessing colony characteristics typical of STPs were scored for each spot (7).

The three observations for each dilution were averaged. This provided a single figure for each replicate of each treatment on each sampling date. The averaged figures were adjusted by log-transformation to stabilize variances and analyzed as a randomized complete block experiment with repeated measurements. Data from both sites were pooled each year to improve precision for analysis.

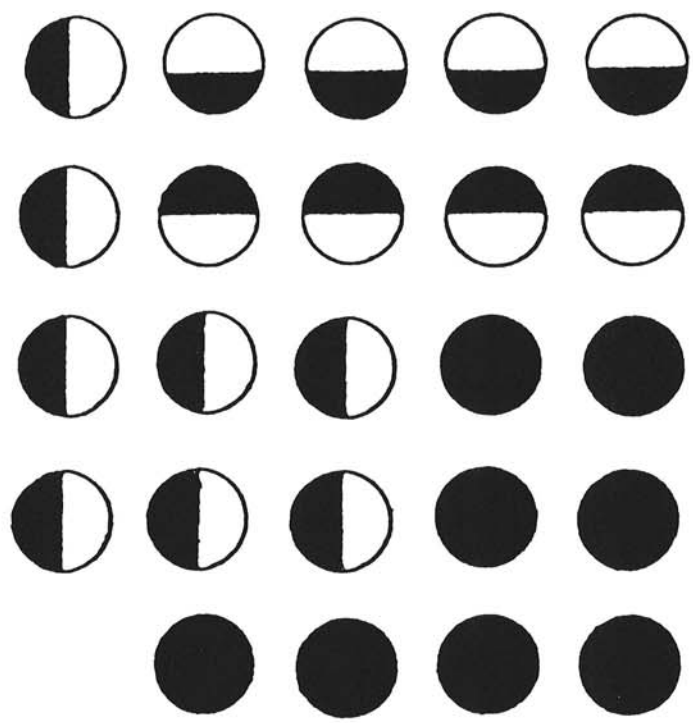

Fig. 1. Example of preparation template for dilution plating, with 24 1-cm orientation circles (three subsamples of eight each).

Characterization and identification of bacterial strains. Suspected STP colonies (15–20 and 20 from each sampling date in 1984 and 1985, respectively) from each experiment were selected randomly and plated onto KB. Pure cultures obtained in 1984 were lyophilized and characterized later. Those obtained in 1985 were characterized immediately after isolation. Cultures (all 24 hr old) that were oxidase negative (11) were streaked or spotted onto mineral salts medium (2) amended with single filter (0.2 μm) sterilized carbon sources (0.1% final concentration) including D-mannitol, myo-inositol, L-tartaric acid, and quinic acid. Quinic acid was used in 1985 only. After 4–7 days of incubation at 22 C, colony growth was compared with cultures grown on nonamended mineral salts medium and to strains that used specific carbon sources (17) (Tables 1 and 2).

Pseudomonad cultures grown on KB for 24 hr at 22 C were also tested for ice nucleation activity. Five milliliters from the initial suspension of each sample was pipetted into each of four (1984) or eight (1985) 15-ml test tubes and placed in a refrigerated methanol bath at −3.5 C, a temperature at which Pss is ice nucleation active but Psp is not. Ice nucleation activity (freezing) was evaluated after 10 min.

A bioassay was conducted with strains possessing characteristics of Psp and Pss by inoculating expanding trifoliate leaves of 3–6-wk-old bean plants (pinto cultivar Olathe) with 24-hr-old cultures grown on KB. A florist's frog was pressed through the leaflet into a sterile gauze pad saturated with a phosphate buffer suspension ($> 10^6$ cfu/ml) of the test culture. Three leaflets on each of three plants were inoculated with each strain. Inoculated plants were placed in a mist chamber at saturated humidity for 24–36 hr at 20–24 C and then moved to a greenhouse bench at 20–26 C under 16 hr of supplemental fluorescent lighting per day. Strains that induced characteristic bacterial water-soaking on inoculated leaflets after 7–10 days were considered pathogenic.

RESULTS

Volunteer beans. In 1984, substantial numbers of volunteer bean plants were found in nine commercial corn (*Zea mays* L.) fields. Epiphytic Psp was recovered from bean volunteers from four fields. Psp was isolated from active lesions on volunteers in three fields, and Pss was isolated from infected foliage in two fields. Psp and Pss were also isolated from infected foliage on volunteer dry beans in one commercial soybean (*Glycine max* (L.) Merrill) field. Volunteer beans were found in a winter wheat (*Triticum aestivum* L.) field in 1984, but STPs were not detected. In 1985, volunteer beans were found in one and nine commercial wheat and corn fields, respectively. STPs were not detected on foliage of the volunteers.

Seedling survey. No STPs were detected on primary leaves of new crop seedlings in 43 commercial dry bean fields surveyed in 1984 or 1985.

Copper efficacy experiments. Both the early and late 1984 spray programs significantly ($P = 0.05$) reduced total and STP bacterial populations on all sampling dates compared with the unsprayed controls (Fig. 2 and Table 3). In 1985, total bacterial populations (Fig. 3) in early sprayed plots were significantly ($P = 0.05$) lower than the controls on each sampling date after the second copper application, and in the late-sprayed plots after the first application. In 1985, STPs were not detected until the next to last sampling date and then only in control plots (Table 3). There were no significant STP or total bacterial population differences between treatments and controls. However, on the final sampling date, STP populations in early and late-sprayed plots were significantly lower ($P = 0.05$) than in control plots (Table 3).

Bacterial strains identified as Psp by carbon source utilization and lack of ice nucleation activity at −3.5 C could consistently infect bioassay plants, causing symptoms indistinguishable from known Psp strains (Table 1). Strains of Pss from this experiment and other sources (Table 1) did not cause water-soaking in the bioassay, a symptom that may (20) or may not (5,18) be associated with development of foliar bacterial brown spot lesions. However, four of five Pss strains collected during this experiment produced lesions typical of Pss strains pathogenic to bean when assayed on detached bean pods (snap bean cultivar BBL 274) (D. E. Legard, *unpublished*).

A pronounced shift occurred in the relative population frequency of each epiphytic pathovar in 1984. Only 10% of the strains characterized as Pss or Psp from the first sampling were Psp as compared with 87% from the last sampling (Table 4). In 1985, 90% of the STP strains were Psp in the final sampling. Ice nucleation activity of bacteria in undiluted suspensions from leaf washings in the copper efficacy experiment were closely related to the frequency of Pss detected by dilution-plating (Table 5). On the first sample date in 1984, when Pss was predominant in the epiphytic community, 59% of the epiphytic bacteria suspensions from unsprayed plots froze at −3.5 C. Subsequent samples froze at steadily decreasing frequencies. The final sample, when Psp was the dominant STP, revealed that only 13% of the suspensions froze. In 1985, ice nucleation activity occurred infrequently (Table 5) and was not related to detectable Pss populations.

During the growing seasons in 1984 and 1985, halo blight was observed on only three or four lightly infected (fewer than 10 lesions each) plants in an unsprayed control plot or buffer rows. No evidence of bacterial brown spot was observed in test plots either year.

DISCUSSION

Epiphytic bacterial populations are lognormally distributed on leaves (8). Thus, when determining mean leaf or leaflet populations from bulked samples, the arithmetic mean is calculated from a skewed (lognormal) distribution. This often results in an

TABLE 1. Pseudomonad strains used to test bioassay and diagnostic schemes

Strain ID	Bean source	Origin of strain
Pseudomonas syringae pv. *syringae*		
F84-1	Pinto	Authors, Colorado
F84-2	Pinto	Authors, Colorado
F84-6	Kidney	Authors, Colorado
F84-10	Pinto	Authors, Colorado
F84-52	Kidney	Authors, Colorado
F84-55	Great northern	Authors, Colorado
Y30	Snap bean	D. J. Hagedorn, Wisconsin
WIS 536	Snap bean	D. J. Hagedorn, Wisconsin
WIS 46	Snap bean	D. J. Hagedorn, Wisconsin
NDA 29	Bean	R. L. Forster, Idaho
Pseudomonas syringae pv. *phaseolicola*		
F82-7	Pinto	Authors, Colorado
F83-18b	Pinto	Authors, Colorado
F84-24D	Pinto	Authors, Colorado
F84-47	Pinto	Authors, Colorado
F84-51	Pinto	Authors, Colorado
F84-57	Kidney	Authors, Colorado
F84-58	Kidney	Authors, Colorado
WIS PSP	Snap bean	D. J. Hagedorn, Wisconsin
RACE 2	Bean	R. L. Forster, Idaho

TABLE 2. Diagnostic characteristics used in identification of *Pseudomonas syringae* pv. *syringae* (Pss) and *Pseudomonas syringae* pv. *phaseolicola* (Psp) from dry bean fields in Colorado in 1984–1985

Diagnostic characteristic	Organism	
	Pss	Psp
Rough-edged colonies	+[a]	+
Blue-green fluorescence	+	+
Oxidase reaction	−	−
Ice nucleation at −3.5 C	+	−
Inositol utilization	+	−
Mannitol utilization	+	−
L-Tartrate utilization	−	−
Quinate utilization	+	+

[a]Indicates positive characteristic or response.

overestimation of the true population mean (9). Leaflet samples were bulked in the copper efficacy experiments and therefore the means were possibly overestimated. Because the experiments were designed to identify differences among treatments rather than specific leaflet population levels, the replicated bulk samples provided a more manageable and efficient procedure than one involving sampling of a multitude of individual leaflets.

Although the estimates of population means may be inflated, we suggest that leaflet populations on the order of 10^5 or 10^6 cfu measured by these methods are indicative of high epiphyte populations on some of the leaflets sampled. In Wisconsin, comparable Pss populations (10^4/g of leaf tissue) on snap beans were associated with the production of bacterial brown spot symptoms (12). It is interesting that such high STP populations in 1984 failed to result in detectable bacterial brown spot or halo blight during the season in Colorado. Hirano and Upper (9) suggested that situations where large populations of epiphytic pathogenic bacteria fail to cause disease "may be due to environmental conditions unfavorable for susceptiblity of the host, survival of epiphytic phytopathogenic bacteria populations, the infection process itself, or a combination of these and other unknown factors." It appears that factors that favor establishment of large epiphytic Psp and Pss populations on bean do not necessarily favor development of halo blight and bacterial brown spot in this region. However, we concur with reports that the probability of foliar bacterial disease incidence increases when epiphytic populations of the pathogen are sufficiently high (9,12,19).

Comparisons of early and late copper spray schedules with unsprayed controls showed that both programs significantly ($P = 0.05$) reduced the STP component of the epiphytic bacterial community on bean leaves. In Wisconsin, populations of Pss at

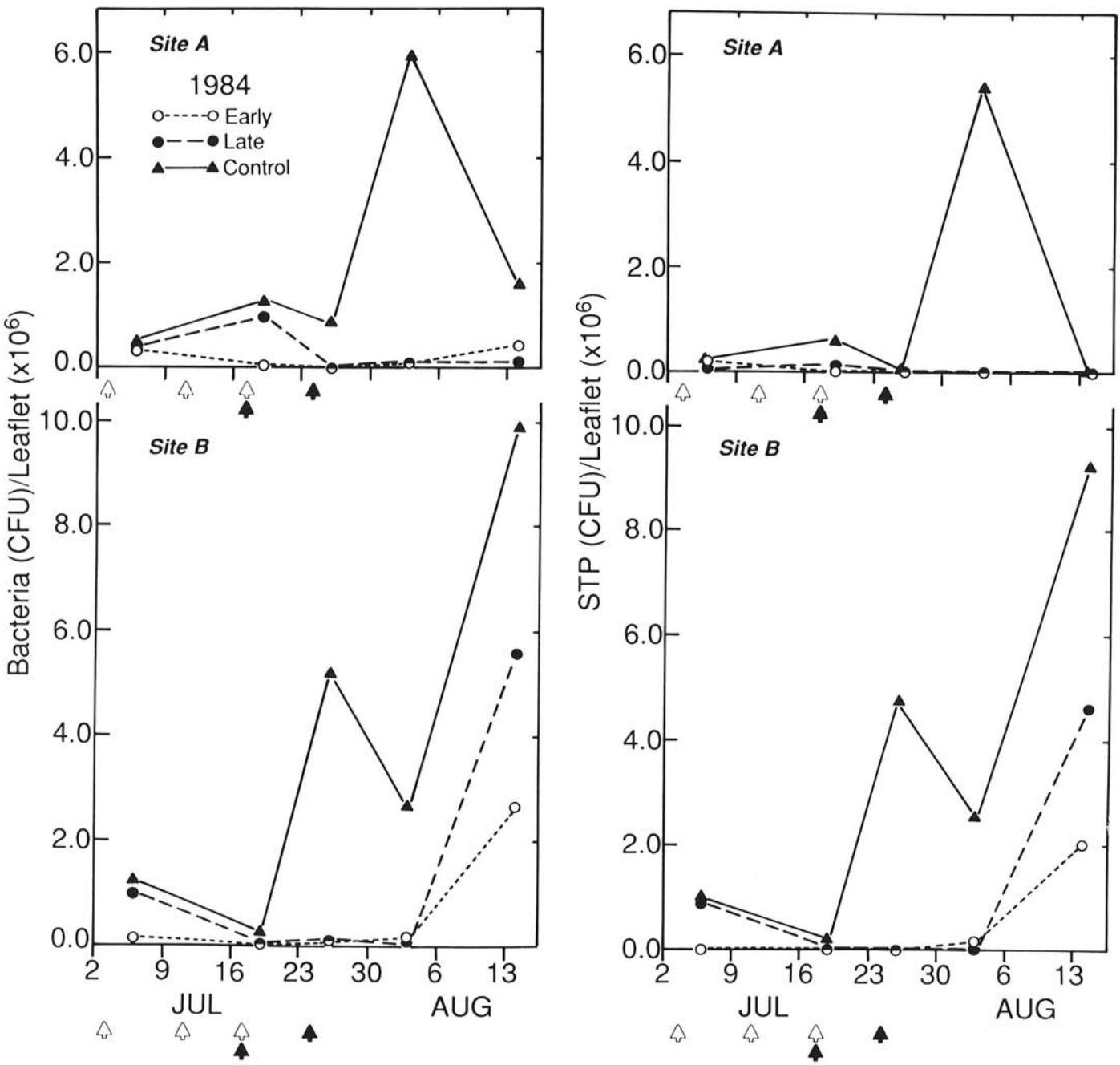

Fig. 2. Average total epiphytic and syringae-type pseudomonad (STP) bacteria per bean leaflet collected at two sites in Colorado in 1984. Each data point is the average of 20 leaflets from each of four replicates. Open and solid arrows indicate early (-------) and late (— — —) cupric hydroxide treatments, respectively. The control treatments are represented by the solid line (——).

high threshold levels have been useful in predicting bacterial brown spot outbreaks (12). Under the environmental and agronomic conditions prevalent during this study, it appears that cupric hydroxide can limit establishment of large epiphytic populations of STPs. This may prevent populations of Psp and Pss from becoming sufficiently high to favor disease development.

In addition to controlling STPs, cupric hydroxide significantly ($P = 0.05$) lowered the overall epiphytic bacterial population of bean leaves. Therefore, judicious use of cupric hydroxide may be applicable in the control of other foliar bacterial diseases of beans by preventing or limiting the establishment of the epiphytic phase of the pathogens.

A discontinuity in the upward trend of bacterial population curves on leaves in control plots was observed at both study sites in both years. This discontinuity appeared to be related to flower initiation. In 1984, plants at site A reached maturity approximately 10 days earlier (July 26) than those at site B, and the corresponding dip in the population curve was observed 1 wk later (August 3) at site B. Such fluctuations may be related to physiological changes in the plant at flower initiation. The sudden decline in the population curves on the last sampling date at site A in 1984 (Fig. 2) was probably because of the earlier maturity of plants at that site and a corresponding decrease in the number of young leaves available to support bacterial epiphytes. Additional work is needed to identify the factors responsible for these fluctuations and to study population dynamics of naturally occurring STPs on other plant parts such as blossoms and pods.

In 1984, there was a shift from a predominantly Pss STP epiphytic initial population to one composed predominantly of Psp later in the season. This increase cannot be attributed to incipient halo blight lesions since symptoms did not subsequently develop. Psp also dominated the STP epiphytic population when STP organisms were detected on the last two sampling dates in 1985. These population trends may help explain the decreased bacterial brown spot and increased halo blight that often occur in late July and early August in our region (H. F. Schwartz and D. E. Legard, *unpublished*).

Traditional field experiments on bactericide efficacy depend on severe disease development for significant treatment differences to

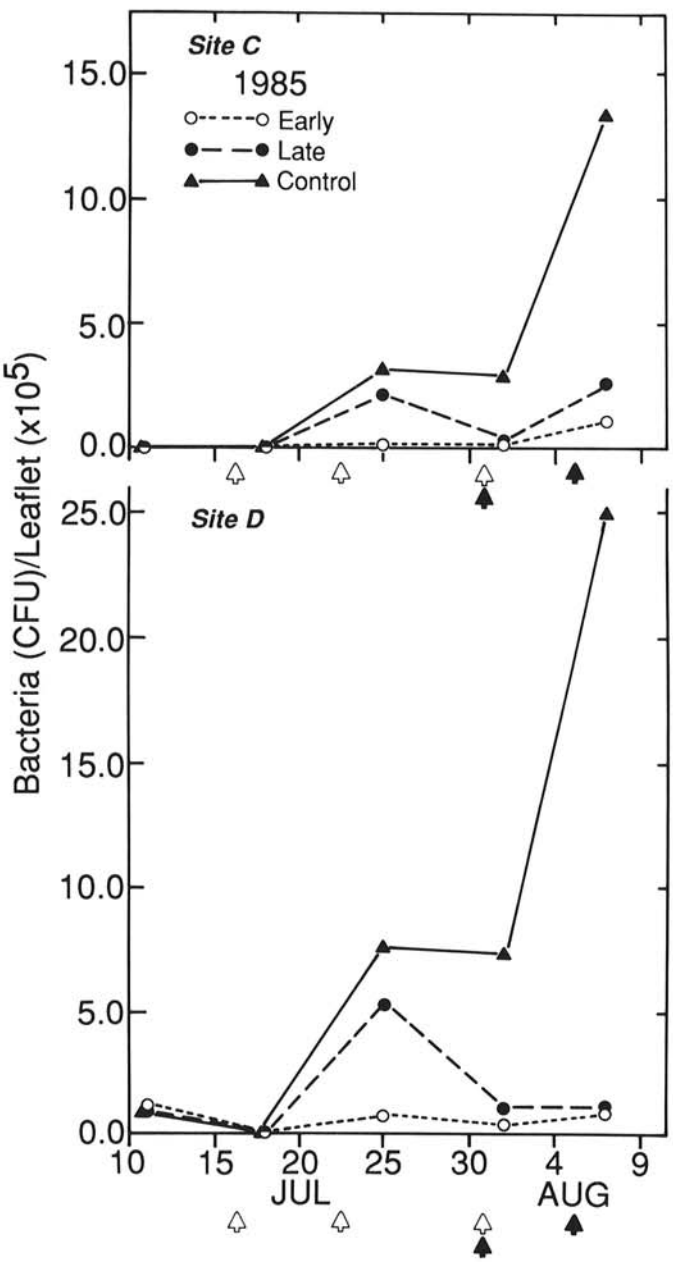

Fig. 3. Average total epiphytic bacteria per bean leaflet collected at two sites in Colorado in 1985. Each data point is the average of 40 leaflets from each of four replicates. Open and solid arrows indicate early (-----) and late (— —) cupric hydroxide treatments, respectively. The control treatments are represented by the solid line (——).

TABLE 3. Comparison of mean log-transformed total bacterial and syringae-type pseudomonad populations (cfu/leaflet) for combined sites in Colorado dry bean fields in 1984 and 1985

Sample number	Total bacteria[y]			STP bacteria[y]		
	Control	Early	Late	Control	Early	Late
1984-1	4.59 a[z]	4.15 b	4.43 ab	3.56 a	1.72 b	3.23 a
-2	4.42 a	3.29 b	3.57 b	2.69 a	0.24 c	1.40 b
-3	4.73 a	3.56 b	3.52 b	2.98 a	0.26 c	1.19 b
-4	5.01 a	3.88 b	3.54 b	4.10 a	1.16 c	0.94 b
-5	5.42 a	4.91 b	4.02 c	3.39 a	2.64 b	2.32 b
1985-1	3.62 a	3.76 a	3.80 a	0.00	0.00	0.00
-2	3.06 ab	2.85 b	3.15 a	0.00	0.00	0.00
-3	4.98 a	3.80 b	4.80 a	0.00	0.00	0.00
-4	4.95 a	3.56 c	3.99 b	0.22 a	0.00 a	0.00 a
-5	5.53 a	4.23 b	4.35 b	1.65 a	0.42 c	0.95 b

[y] Data are the log-transformed means of four replicates each from two sites both years.

[z] Bacterial means (total or STP) within a row followed by the same letter are not significantly different ($P = 0.05$) according to the FLSD test.

TABLE 4. Percentage of syringae-type pseudomonad (STP) strains identified as *P. syringae* pv. *phaseolicola* (Psp) from dry bean fields in Colorado in 1984 and 1985

Sample number	Psp strains isolated (%)	
	1984	1985
1	10	...[a]
2	20	...
3	50	...
4	56	...
5	87	90

[a] Zero or negligible number of STPs detected.

TABLE 5. Supernatants from undiluted leaf washings that froze after 10 min at −3.5 C in copper efficacy experiments on dry bean leaves from Colorado in 1984 and 1985

Sample number	Application treatment					
	1984			1985		
	Control	Early	Late	Control	Early	Late
1	59	44	57	0	2	0
2	41	16	16	0	0	0
3	38	6	13	0	0	14
4	34	0	0	3	0	2
5	13	0	6	11	0	2

be expressed. The ability to monitor populations of foliar bacterial epiphytes provides support for, or a viable alternative to, traditional evaluation procedures. Determining bactericide efficacy by studying effects on epiphyte populations can provide useful and important epidemiological and control data even in the absence of visible symptoms.

The presence of volunteer beans contaminated or infected with Psp and Pss in the northeastern Colorado bean production region may be an important factor in the epidemiology of halo blight and bacterial brown spot. Volunteer bean seedlings were found in corn fields as early as mid-May, a month before seedling emergence in commercial bean fields. Psp and Pss were frequent inhabitants (as epiphytes or pathogens) of volunteer bean foliage, suggesting that unharvested seeds may provide an excellent overwintering site for both pathogens. Under favorable weather conditions, the bacteria may be disseminated by windblown rain or aerosols and become established on emerging bean seedlings in nearby commercial fields.

In 1985, no STPs were found on volunteer beans. This lack of epiphytic STPs may be attributed to the reduction in incidence and severity of halo blight and bacterial brown spot observed in the region in 1984. This reduction should result in a decrease of STPs harbored on seeds (volunteers) that remained in fields after harvest. In addition, unusually low rainfall during June and early July in 1985 (Fig. 4) probably restricted colonization and growth of STPs on volunteers, thereby reducing bacterial dispersal to nearby fields. It appears that volunteer beans are an important source of Psp and Pss inocula, especially in years after severe halo blight and bacterial brown spot outbreaks, such as that which occurred in 1983 (H. F. Schwartz, *unpublished*).

Lack of epiphytic STPs on new crop bean seedlings in commercial fields planted with certified seed suggests that western-grown certified seed stocks are relatively free of STP contamination. However, it is possible that epiphytic populations of Pss and Psp on recently emerged seedlings may be smaller than we could detect, or were not found because of the limited number of leaves sampled.

Pss strains isolated from all epiphyte experiments, as well as known pathogenic strains (Table 1), failed to cause visible water-soaking under greenhouse conditions. These results suggest that our greenhouse environment was not favorable for bacterial brown spot symptom development or alternatively that foliar water-soaking is not an appropriate criterion for determining pathogenicity of Pss. However, because some Pss strains from this experiment were pathogenic to bean in a detached pod bioassay, we suggest that the Pss component of the STP populations described herein were capable of causing bacterial brown spot under suitable conditions in the field.

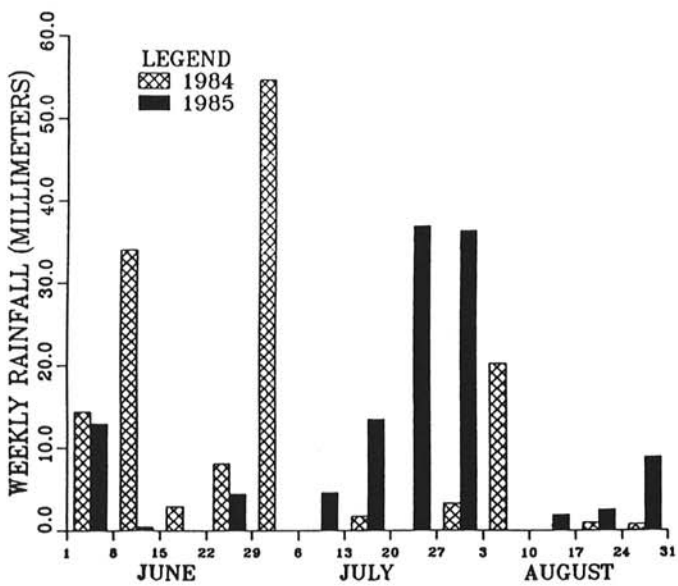

Fig. 4. Weekly rainfall (mm) at Holyoke, CO, in 1984 and 1985.

Data from this study illustrate that in northeastern Colorado cupric hydroxide can prevent or delay establishment of high STP epiphytic populations. Because epiphytic phytopathogenic bacteria can provide inoculum for disease, the probability of disease increases as epiphyte populations increase. Therefore, consideration of epiphyte population dynamics for timing of bactericide applications could provide more consistent and effective control of halo blight and bacterial brown spot.

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