Effect of Host on Multiplication and Distribution of Bean Common Blight Bacteria

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ABSTRACT

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Populations of rifampin-resistant *Xanthomonas phaseoli* (= *X. campestris*) (*Xp*) were determined in and on leaves and pods of resistant (tepary bean [*Phaseolus acutifolius*]), moderately resistant (breeding line MSU-51319 and Great Northern-type cultivar Valley [both *P. vulgaris*]) and susceptible bean hosts (cultivars Seafarer and Tuscola [both *P. vulgaris*]) by using a rifampin-containing medium. While bacterial multiplication patterns were similar for leaves and pods of moderately resistant and susceptible cultivars, maximum bacterial populations were generally lower in the former, particularly during the reproductive stage of plant development. High *Xp* populations were detected in and on uninoculated, symptom-free leaves of both susceptible and moderately resistant hosts, but not in or on those of resistant genotypes. Systemic colonization of plants by *Xp* throughout the growing season was greatest in the susceptible genotypes, intermediate in the moderately resistant genotypes, and absent in the resistant genotype.

Additional key words: bacterial bean disease, disease resistance.

Common blight, caused by *Xanthomonas phaseoli* (E. F. Smith) Dowson (= *X. campestris*) (*Xp*) is considered one of the most serious seedborne diseases of dry edible and green beans in many production areas throughout the world (5,27). Although practical short-term control is possible by using disease-free seed and crop rotation, long-term control depends on the development of disease-resistant cultivars. Considerable effort has been directed toward finding resistant germplasm useful for breeding (5,17); the absence of immunity to common and fuscous blights further contributes to the importance of blight in bean production.

Epiphytic survival and multiplication on surfaces of host and nonhost plants has been described for several plant pathogenic bacteria (8,12,13,15,19,21,22). Our previous studies indicated that most of the germplasm sources used in bean breeding programs throughout the world may be potential "symptomless carriers" of *Xp*, the common blight pathogen (3). The data were consistent with the conclusions of previous reports that large populations of bacteria may develop in inoculated leaves of lines and cultivars with intermediate levels of resistance, although the disease reactions developed differ from those of susceptible cultivars (6,11,20).

An important finding in our preliminary studies was that *Xp* can systemically colonize the uninoculated leaves of all germplasm sources, frequently with the development of few or no visible disease symptoms, and that the bacteria are differentially affected in hosts of different genotypes.

This investigation compared the multiplication and distribution of *Xp* in bean hosts of different genotypes and of different levels of disease resistance.

MATERIALS AND METHODS

The experiments were conducted under field conditions at the Botany and Plant Pathology Research Farm, Michigan State University, East Lansing, during the summers of 1977 and 1978.

Host genotypes. Hosts with the following genotypes were used: navy bean (*Phaseolus vulgaris* L.) cultivars Seafarer and Tuscola (susceptible to common blight); MSU-51319 (an MSU breeding line) and Great Northern-type cultivar Valley, both *P. vulgaris* (moderately resistant); tepary beans (*P. acutifolius* A. Gray) P597, and cultivar Arizona-Buff (resistant).

Bacterial isolate. A spontaneous mutant (R15-1) of *Xp* resistant to 50 ppm rifampin, obtained by conventional selective plating methods and found to be as virulent on beans as the parental wild type (*Xp* 15, a highly virulent Michigan isolate), was used throughout these experiments (3).

Experimental plots. Disease-free seeds of the different hosts were planted by hand in three-row plots 3 m long and 50 cm apart; in-row seed spacing was 7 cm. There were three replications of each treatment in all experiments.

Inoculation technique. Suspensions of R15-1 were prepared from 48-hr YCA cultures (YCA: 10 g of yeast extract, 15 g of agar, and 2.5 g of calcium carbonate in 1,000 ml of glass-distilled water) by rinsing the bacteria off the agar surface and suspending them in sterile distilled water. Plants were inoculated by gently spraying the lower and upper surfaces of primary leaves, trifoliolate leaves, or pods to runoff with a knapsack sprayer containing a bacterial suspension of $1–5.0 \times 10^7$ cells per milliliter. Leaves or pods were not watersoaked during inoculation. This procedure deposited about 0.021 ml of inoculum per square centimeter of leaf area (determined by weighing leaflets of known area before and after inoculation).

Multiplication of *Xp* in and on bean leaves and pods. Populations of the R15-1 mutant of *Xp* in and on inoculated trifoliolate leaves and pods of different bean hosts were monitored in field experiments during the 1977 and 1978 growing seasons. Samples of 21 inoculated trifoliolate leaves or 21 pods taken at random from each replication at each assay period were lightly shaken for 1 min in 100 ml of 0.01 M phosphate buffer, pH 7.2 (to remove and measure surface populations), and then homogenized in the same amount of buffer in a Waring Blendor (to measure internal populations). After appropriate serial dilutions, suspensions were plated on YCA supplemented with 50 μg/ml

rifampin and 25 μg/ml cycloheximide; colonies were counted after 4 days of incubation at 24 ± 1 C. Total populations were the sum of surface plus internal populations.

Bacterial multiplication and movement within different bean hosts were studied in inoculated seedlings with fully expanded primary leaves. Successive leaves on the main axis were assayed for the presence of the mutant; assay samples consisted of 15 leaflets per replication. At the reproductive stage (well-filled plump pods), five plants from each replication were assayed for the presence of the mutant in roots and stems by the same procedure used for leaves and pods. Tissues were previously surface sterilized (5 min in 2.5% NaOCl) and rinsed in sterile distilled water.

Populations of *X. phaseoli* are expressed as the number of colony-forming units (CFU) per 100 cm^2 of leaf tissue (approximate average area of one leaf) or per 10 cm^2 of pod tissue (approximate average area of one pod).

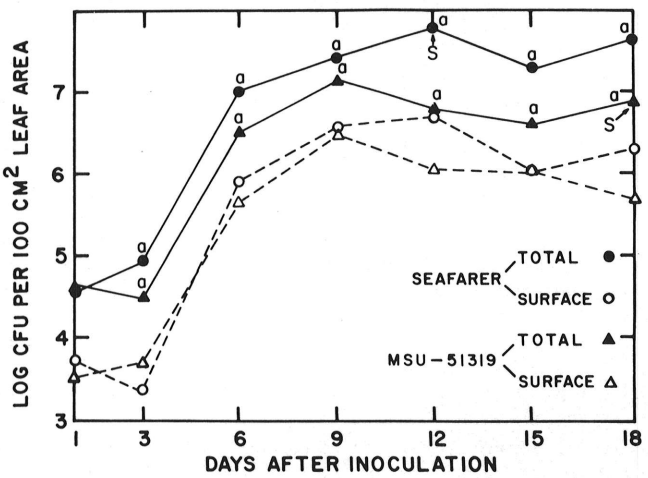

Fig. 1. Total and surface populations of *Xanthomonas phaseoli* (R15-1 mutant) associated with trifoliolate leaves of moderately resistant (MSU-51319) and susceptible (Seafarer) bean hosts. Twenty-three-day-old plants (third and fourth trifoliolate leaves) were inoculated to runoff with a suspension of R15-1 (1.0×10^7 cells per milliliter) at day 0. Values are averages of three replications. Means for the same day with the same letter are not significantly different at $\alpha = 0.05$ by Tukey's w-procedure. S = symptoms.

RESULTS

Leaf populations, 1977. Total and surface populations of *Xp* associated with leaves of moderately resistant MSU-51319 and susceptible Seafarer are shown in Fig. 1. Total populations followed a typical bacterial multiplication curve with a 3-day lag phase and a 6-day logarithmic or exponential phase with mean generation (or doubling) times of 17.1 hr and 15.1 hr for MSU-51319 and Seafarer, respectively. A stationary phase then followed in which populations remained stable or declined slowly (Fig. 1). Surface populations followed a similar pattern and ranged from 7.6 to 25.1% of the total population on MSU-51319 and from 2.6 to 18.7% on Seafarer. Although peak populations were lower in the moderately resistant MSU-51319, primarily during the floral development stage, analysis of variance revealed no significant differences for genotype and genotype × time interactions. In both hosts, symptoms developed during the flower stage of development, about the time when peak bacterial populations were obtained. Disease developed later and was less severe in MSU-51319 than in Seafarer.

Total and surface populations associated with leaves of P597 and Seafarer were similar until 16–28 days after inoculation (Fig. 2). In the host with resistant tepary genotype (P597), maximum total numbers of bacteria occurred 16 days after inoculation and then declined. In susceptible Seafarer, populations continued to increase and were significantly higher than those for P597 at 28 days after inoculation. The *Xp* populations on leaf surfaces of both hosts varied throughout the experiment, ranging from 4.3 to 27.0% of the total population on P597 and from 1.0 to 16.7% on Seafarer. There were no visible disease symptoms on plants of P597.

Pod populations, 1977. Total and surface populations of *Xp* associated with pods of MSU-51319 and Seafarer are shown in Fig. 3. Bacterial multiplication in both hosts exhibited a 4-day lag phase followed by a 4-day exponential phase. In MSU-51319, mean generation time was 23.7 hr during this phase; populations peaked at 8 days after inoculation, and then slowly declined. In susceptible Seafarer, bacteria remained in the exponential multiplication phase for about 8 days. The bacteria entered a stationary phase at 12 days after inoculation, and populations continued to increase slowly. Surface populations of *Xp* on pods of MSU-51319 ranged from 60 to 70.6% of the total populations throughout the assay period. On susceptible Seafarer, surface populations were 61.5% at day 1 and 86.2% at day 8, but they had decreased to 28% of the total population at day 16. Symptoms were first observed in Seafarer at

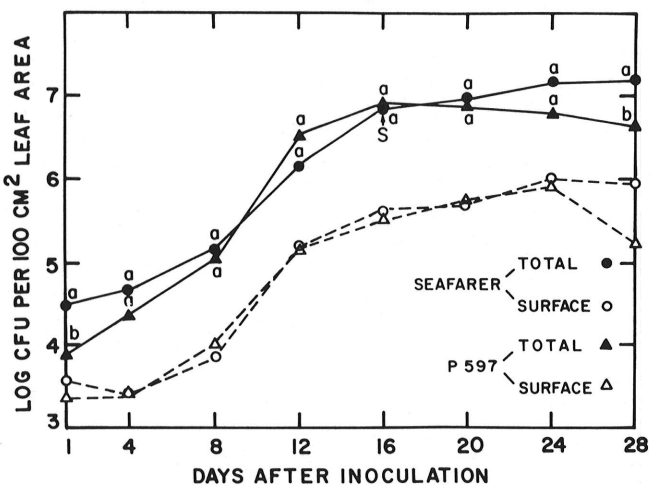

Fig. 2. Total and surface populations of *Xanthomonas phaseoli* (R15-1 mutant) associated with trifoliolate leaves of resistant (P597) and susceptible (Seafarer) bean hosts. Thirty-six-day-old plants (third and fourth trifoliolate leaves) were inoculated to runoff with a suspension of R15-1 (1.0×10^7 cells per milliliter) at day 0. Values are averages of three replications. Means for the same day with the same letter are not significantly different at $\alpha = 0.05$ by Tukey's w-procedure. S = symptoms.

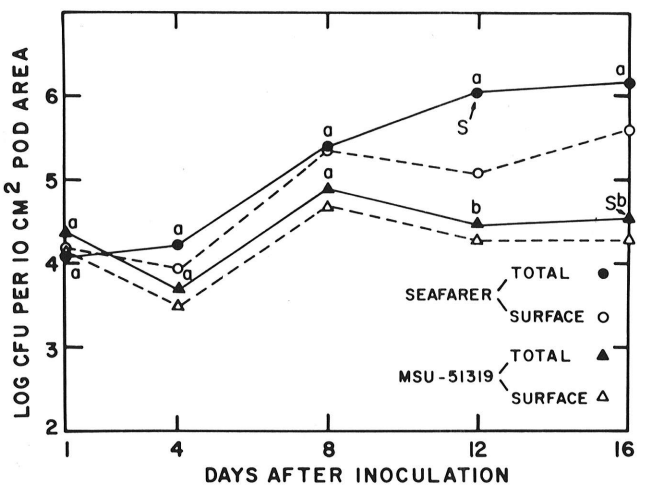

Fig. 3. Total and surface populations of *Xanthomonas phaseoli* (R15-1 mutant) associated with pods of moderately resistant (cultivar MSU-51319) and susceptible (cultivar Seafarer) bean hosts. Pods (flat-pod stage) were inoculated by gentle spraying to runoff with a suspension of R15-1 (1.0×10^7 cells per milliliter) at day 0. Values are averages of three replications. Means for the same day with the same letter are not significantly different at $\alpha = 0.05$ by Tukey's w-procedure. S = symptoms.

12 days after inoculation. Disease symptoms in MSU-51319 were observed only at the end of the assay period and were much less severe.

Leaf populations, 1978. Total and surface populations of *Xp* associated with leaves of resistant tepary cultivar Arizona-Buff, moderately resistant Valley, and susceptible Tuscola bean hosts are shown in Fig. 4. Differences in bacterial multiplication patterns were evident shortly after inoculation. In tepary bean, total *Xp* populations increased only slightly during the first few days after inoculation and then remained in stationary phase. In Valley, populations showed a 4-day lag phase and then increased exponentially for 8 days with a mean generation time of 15.2 hr. They peaked on day 12 and then entered a stationary phase. No lag phase was evident in Tuscola; bacterial populations increased exponentially with a mean generation time of 16.4 hr until 8 days after inoculation, then entered a stationary phase. Bacterial populations on leaf surfaces showed multiplication patterns similar to those of total populations, ranging from about 1 to 7.5% of the total population on tepary, 15 to 28% on Valley, and 6.6 to 15.0% on Tuscola.

Total and surface populations of *Xp* associated with uninoculated leaves of Valley and Tuscola were similar to those previously found in and on inoculated tissue. Practically no bacteria were found associated with uninoculated leaves of tepary bean. Disease symptoms were initially recorded in Tuscola at the early flower stage of plant development; symptoms in Valley developed later and were less severe, and no symptoms were observed in tepary.

Pod populations, 1978. Total and surface populations of *Xp* associated with pods of the three hosts are presented in Fig. 5. Total bacterial populations were similar for Valley and Tuscola, although populations were usually lower in the former. After a 4-day lag phase, bacteria multiplied exponentially for 4 days with mean generation times of 21.2 hr and 19.0 hr for Valley and Tuscola, respectively. At day 8, populations entered a stationary phase in Valley, but continued to increase slowly in Tuscola. Bacterial populations in tepary bean changed little during the first 8 days, and then gradually decline.

On tepary and Valley bean plants, pod surface populations of *Xp* represented high percentages of the total populations, ranging from 71.4 to 81% and 50.8 to 84%, respectively. On susceptible Tuscola, pod surface populations of *Xp* were high until day 4, but represented less than 30% of the total population for the remainder of the experimental period. No Xanthomonas blight symptoms were observed on pods of tepary bean; only a few blight lesions were seen on pods of Valley at the end of the experiment.

Multiplication, movement, and distribution of *Xp* in resistant, moderately resistant, and susceptible bean hosts. Multiplication and movement of the R15-1 mutant of *Xp* were studied in inoculated seedlings of the different bean hosts throughout the growing season of 1978. Total populations of *Xp* from primary leaves until the early reproductive stage of plant development are presented for individual leaves that successively differentiated from the main axis (Table 1). In resistant tepary bean plants, *Xp* was associated consistently only with inoculated primary leaves. In moderately resistant cultivar Valley, bacteria were recovered from primary and first, second, and third plus fourth trifoliolate leaves. In susceptible Tuscola, bacteria were isolated from primary and first, second, third plus fourth, fifth, and sixth trifoliolate leaves. High bacterial populations and the development of symptoms were associated first with the older leaves and later the younger ones, from the primary to the second trifoliolate leaves in Valley and from the primary to the fifth trifoliolate leaves in Tuscola. No symptoms and low levels of bacteria were isolated from inoculated and first trifoliolate leaves of resistant tepary bean plants.

Bacteria systemically colonized stems of Valley and Tuscola plants, but not those of tepary bean (Table 2). The *Xp* populations recovered from mature plants of Valley and Tuscola were 1.2×10^2 and 6.5×10^4 CFU per gram of stem tissue, respectively. No evidence of infection was observed on stems of either genotype. Bacteria were recovered from the roots of only Tuscola, and that recovery was at low population levels and not consistent. The results of all attempts to isolate *Xp* from flowers of the different genotypes throughout the growing season were negative. The *Xp* bacteria were recovered from the pods and seeds of Tuscola and Valley plants with visible symptoms.

DISCUSSION

Total and surface populations of the R15-1 rifampin-resistant mutant of *Xp* associated with leaves of susceptible and moderately resistant bean hosts resembled typical bacterial multiplication curves, with a 3- to 4-day lag phase followed by a logarithmic or exponential phase 4–12 days long and then by a stationary phase. Mean generation times during exponential multiplication ranged from 15.1 to 21.2 hr in leaves and from 23.7 to 36.6 hr in pods. While *Xp* populations were similar from leaves and pods of moderately-resistant and susceptible hosts, maximum populations

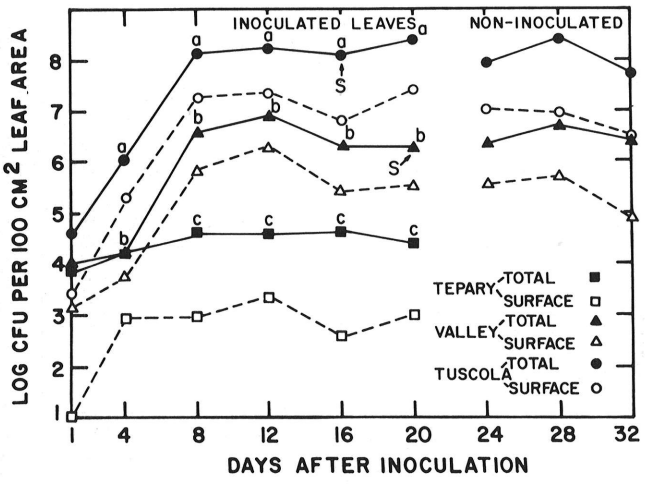

Fig. 4. Total and surface populations of *Xanthomonas phaseoli* (R15-1 mutant) associated with trifoliolate leaves of resistant (tepary cultivar Arizona-buff), moderately resistant (cultivar Valley) and susceptible (cultivar Tuscola) bean hosts. Twenty-five-day-old plants (second and third trifoliolate leaves) were inoculated to runoff with a suspension of R15-1 (1.0×10^7 cells per milliliter) at day 0. Values are averages of three replications. Means for the same day with the same letter are not significantly different at $\alpha = 0.05$ by Tukey's w-procedure. S = symptoms.

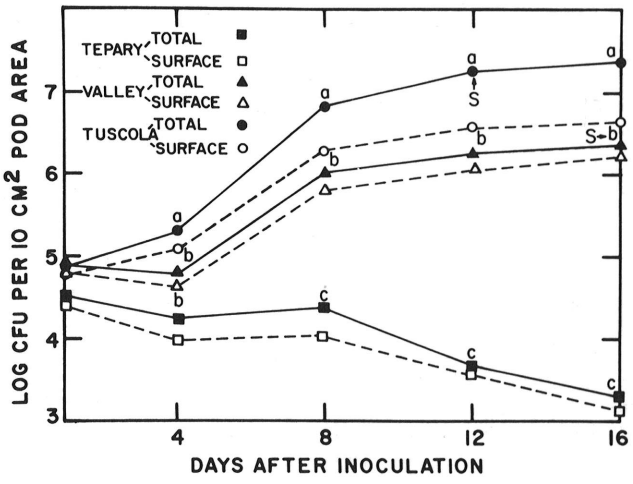

Fig. 5. Total and surface populations of *Xanthomonas phaseoli* (R15-1 mutant) associated with pods of resistant (tepary cultivar Arizona-Buff), moderately resistant (cultivar Valley), and susceptible (cultivar Tuscola) bean hosts. Pods (flat-pod stage) were inoculated by gently spraying to runoff with a suspension of R15-1 (1.0×10^7 cells per milliliter at day 0. Values are averages of three replications. Means for the same day with the same letter are not significantly different at $\alpha = 0.05$ by Tukey's w-procedure. S = symptoms.

TABLE 1. Population levels of *Xanthomonas phaseoli* (R 15-1 mutant) in leaves of resistant (tepary bean cultivar Arizona-Buff), moderately resistant (cultivar Valley), and susceptible (cultivar Tuscola) bean hosts

Host cultivars and leaf	CFU per 100 cm^2 leaf area at indicated days after inoculation[a]									
	1	4	7	10	14	18	22	26	30	34
Tepary										
Primary leaves	9.3×10^3	3.3×10^5	2.8×10^6	1.8×10^6	3.4×10^6	3.1×10^4	1.0×10^4	ab[b]	ab	ab
First trifoliolate	···	···	1.0×10^1	1.0×10^1	$<1.0 \times 10^1$	$<1.0 \times 10^1$	0.0	0.0	0.0	ab
Valley										
Primary leaves	8.1×10^3	2.3×10^4	1.1×10^6	5.8×10^5	2.3×10^6	$(3.0 \times 10^5$[c])	(1.6×10^5)	ab	ab	ab
First trifoliolate	···	···	6.4×10^3	6.9×10^4	1.2×10^6	8.7×10^5	1.0×10^6	7.3×10^6	(1.9×10^5)	ab
Second trifoliolate	···	···	···	···	7.8×10^4	2.4×10^4	1.5×10^6	2.0×10^4	4.3×10^5	(5.3×10^5)
Third and fourth trifoliolate	···	···	···	···	···	0.0	0.0	0.0	0.0	1.3×10^2
Tuscola										
Primary leaves	1.5×10^4	5.6×10^5	4.8×10^6	9.0×10^6	1.8×10^7	(2.6×10^7)	(1.8×10^7)	ab	ab	ab
First trifoliolate	···	···	6.7×10^5	5.9×10^6	1.6×10^7	2.3×10^7	(2.2×10^7)	(4.0×10^7)	(3.2×10^7)	ab
Second trifoliolate	···	···	···	···	1.1×10^6	4.8×10^6	1.5×10^6	(4.0×10^6)	(6.7×10^5)	(1.0×10^6)
Third and fourth trifoliolate	···	···	···	···	···	2.1×10^3	3.2×10^5	1.4×10^5	(1.5×10^7)	(1.0×10^5)
Fifth trifoliolate	···	···	···	···	···	···	4.7×10^2	7.0×10^3	1.8×10^4	(1.3×10^7)
Sixth trifoliolate	···	···	···	···	···	···	···	0.0	6.7×10^3	1.7×10^5

[a] Fourteen-day-old plants (seedling stage) were inoculated by gentle spraying of the primary leaves to runoff with a suspension of R15-1 (1.0×10^7 cells per milliliter). Values are averages of three replications. CFU = colony forming units.
[b] ab = abscised.
[c] Parentheses indicate presence of macroscopic disease symptoms.

TABLE 2. Recovery of *Xanthomonas phaseoli* (R15-1 mutant) from various plant parts after inoculation of the primary leaves of resistant (tepary bean cultivar Arizona-Buff), moderately resistant (cultivar Valley), and susceptible (cultivar Tuscola) bean hosts[a]

Host	Bacterial growth on YCA-rifampin media[b]									
			Trifoliolate leaves							
	Root	Primary leaves	1st	2nd	3rd + 4th	5th	6th	Stems[c]	Flowers	Pods[d]	Seeds[d]
Tepary	−	+	+	−	−	−	−	−	−	−	−
Valley	−	+	+	+	+	−	−	+	−	+	+
Tuscola	+	+	+	+	+	+	+	+	−	+	+

[a] Fourteen-day-old plants (seedling stage) were inoculated by gentle spraying of the primary leaves to runoff with a suspension of R15-1 (1.0×10^7 cells per milliliter).
[b] Data were taken from five single-plant replications.
[c] Bacteria isolated from surface-sterilized stems.
[d] Bacteria recovered only from pods and seeds with visible blight symptoms.

were generally lower in the former, particularly during the reproductive stage of plant development. At this time, the exponential phase of bacterial multiplication in resistant hosts abruptly terminated and the population then declined and remained stable. In susceptible hosts, bacterial multiplication continued, but at a lower rate.

In general, multiplication patterns of *Xp* in tissues of resistant and susceptible genotypes agree with those reported for this (6,11,20) and for other phytopathogenic bacteria (8,10,16,19,22). Pathogen populations increase after inoculation irrespective of the host genotype, but the increase is less in resistant than in susceptible plants.

However, bacterial multiplication patterns in resistant tepary bean cultivar Arizona-Buff differed from those in the other hosts in that *Xp* survived in inoculated tissues for relatively long periods of time, but remained at the stationary phase or declined slowly after inoculation. While it has previously been suggested that *Xp* may multiply in tepary bean (23,25), this is the first description of population trends of the bacteria under field conditions.

Population trends of blight bacteria on the surface of leaves of resistant and susceptible hosts were similar to those of total populations and, except for tepary Arizona-Buff, large numbers of bacteria were available for dissemination early in the infection process. For example, on the surfaces of leaves of resistant hosts epiphytic bacteria averaged more than 65% of the total population throughout the assay period. In blight-susceptible hosts, most of the bacterial populations were internal after 12 days.

It has been suggested that both external and internal factors affect multiplication of bacteria in and on leaves and pod tissues of resistant bean cultivars (7,9,18,19). Independent genetic control of the differential reaction of foliage and pods of bean to *Pseudomonas phaseolicola* (14) and to *Xp* (4,7) has been reported. The importance of obtaining resistance in both leaves and pods to these pathogens has been emphasized (6).

Our results clearly indicate that even though large populations of *Xp* were associated with inoculated leaves and pods of moderately resistant bean genotypes, the disease reactions on the resistant genotypes were less severe than those on the susceptible genotypes. The visible appearance of blight symptoms in the genotypes coincided closely with the transition from the exponential to the stationary phase of bacterial multiplication; however, the incubation period necessary to attain the threshold population for symptom expression was longer in resistant than in susceptible plants. High *Xp* populations also were associated with uninoculated symptom-free leaves of both susceptible and moderately resistant hosts, which suggests that *Xp* may undergo a "resident phase" of growth in both. Such a multiplication phase suggests that inoculum for secondary spread of *Xp* may develop in the absence of visible disease symptoms. In fact, no visible Xanthomonas blight symptoms were ever found on leaves or pods of tepary beans during this study, a finding that agrees with previous reports (23,25).

That *Xp* may move systemically in infected bean plants was previously reported by Barlow (1), Burkholder (2), and Zaumeyer and Thomas (26,27). Recently, Weller (24) determined that all above and below-ground portions of seedlings grown from internally infected seeds were colonized by the blight bacteria immediately after germination. Spread of the bacteria in the expanded leaf canopy was facilitated by rain, bud colonization, and

systemic movement. According to Weller, the overall rate at which bean plants are colonized is strongly affected by the multiplication rate of the bacterial population on each infected leaf.

Results of our preliminary greenhouse experiments (3) and the present field studies have shown that systemic colonization of bean plants by *Xp* is affected by genotype of the host. Our results are consistent with the general pattern of bean blight colonization of susceptible plants as reported by Weller (24). Patterns of *Xp* colonization were similar in moderately resistant and suceptible hosts, although the bacteria multiplied more slowly in the moderately resistant hosts. Thus, in moderately resistant plants, levels of inoculum for systemic and rain-splashing spread were lower, and the bacteria tended to remain close to the primary site of infection. In the resistant tepary bean, bacteria were detected consistently only in the inoculated primary leaves. Additional studies are necessary to determine the mechanisms involved in tepary bean that limit the multiplication and spread of blight bacteria.

Our findings may be important to bean breeders and seed producers. Heretofore, plant pathologists and breeders have selected for disease resistance on the basis of symptom development and severity. Bean breeding programs directed to the development of Xanthomonas blight resistance should include tests to monitor the leaf, pod, and seed populations of the pathogen. Tepary bean (*Phaseolus acutifolius*) continues to be the best source of blight resistance presently available; certain accessions had the highest foliage and pod resistance of the germplasm tested to a range of *Xp* isolates (3) and also have shown resistance to systemic colonization by the bacteria. Breeding programs should emphasize the transfer of this resistance to *Phaseolus vulgaris* through interspecific hybridization.

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