

## Analysis of Spore Dispersal Gradients of *Botrytis cinerea* and Gray Mold Disease Gradients in Snap Beans

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### ABSTRACT

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Spore dispersal, spore incidence on blossoms, and pod rot disease gradients from point inoculum sources of *Botrytis cinerea* were measured over time in two snap bean (*Phaseolus vulgaris*) fields. Laboratory-grown inoculum was placed at ground level in a 30 × 30-cm square at bloom initiation and removed at full bloom. Dispersal of inoculum, assessed by quantifying the number of viable spores washed from bean foliage, was limited to within 3 m from the inoculum source during bloom. At harvest, the spore populations on plants were 20–30 times higher than populations at full bloom due to production of secondary inoculum. During the bloom period, incidence of *B. cinerea* on senescing blossoms averaged 70% at a

distance of 0.9 m from the inoculum source, but <25% at distances greater than 4 m. In one experiment, the incidence of pod rot at harvest averaged 7.2% at 0.9 m from the inoculum source, but only 1.3% at 4.5 m. Spore dispersal gradients (log spore number versus log distance) showed significant flattening at harvest compared to full bloom, whereas gradients for pod rot incidence at harvest did not flatten compared to incidence of *B. cinerea* on blossoms at full bloom. Because senescing blossoms are the primary infection court for infection of the pods, the nonsignificant flattening of the pod rot gradient suggests that early arrival of inoculum of *B. cinerea* on blossoms was important in pod rot development.

*Additional key word:* epidemiology.

Gray mold of snap beans (*Phaseolus vulgaris* L.) caused by *Botrytis cinerea* Pers. ex Fr. is a perennial problem in Oregon's Willamette Valley. The disease, which results in a watery soft rot of the bean pods, affects the quality of the crop and results in direct losses to growers and processors. In the past, disease control has been achieved with applications of foliar fungicides; however, erratic disease development under "normal" crop management conditions, coupled with resistance of *B. cinerea* to benomyl (20) and lack of other efficacious compounds for control, have discouraged fungicide use.

Recently, efforts have been made to predict the occurrence of gray mold of snap beans (6), but little is known about the source of primary inoculum. Several researchers have demonstrated the importance of local inoculum sources in the epidemiology of diseases caused by *Botrytis* spp. Ellerbrock and Lorbeer (4) reported that nearby seed production fields, cull piles, and within-field sclerotia were primary inoculum sources in *Botrytis* leaf blight of onions. Most infections of *B. cinerea* in strawberries originate from nearby sources of inoculum (12,15). In New York, ascospores of *Botryotinia fuckeliana* (De Bary) Whetz., the perfect stage of *B. cinerea*, produced in apothecia in snap bean fields may serve as a primary inoculum source in gray mold of beans (16).

In Oregon, apothecia of *B. fuckeliana* have not been found in snap bean fields in the Willamette Valley, but sclerotia frequently form on crop debris (11). Occasionally a gray mold seedling blight occurs on beans (11,21). Infected seedlings bear conidia of *B. cinerea* for extended periods, thereby serving as a local inoculum source (11). In addition, colonized senescent bean blossoms lying on the soil surface produce large amounts of secondary inoculum (11).

The purpose of this study was to determine the importance of within-field inoculum sources in gray mold of beans by: characterizing *B. cinerea* spore dispersal, spore incidence on

blossoms, and pod rot disease gradients from point sources of inoculum; and determining the relative importance of primary and secondary inoculum in disease development.

### MATERIALS AND METHODS

**Plot description.** Two 0.4-ha plots of snap bean cultivar "OSU 1604" were established in a Chehalis silty-clay loam soil located on the Oregon State University (OSU) Vegetable Crop Research Farm, near Corvallis. The first plot was planted on 26 June 1981, and the second on 20 July 1981. Seed was sown in 90-cm rows at a rate of 79 kg/ha. The rows in all plots were band fertilized at planting with 8-24-8 (N-P-K) at 672 kg/ha. Weed control in both plots consisted of trifluralin (0.84 kg a.i./ha, preplant), dinitroamine (6.72 kg a.i./ha, preemergence), and one cultivation approximately 4 wk after planting. Insect control consisted of fonofos (2.24 kg a.i./ha) at planting for *Scutigerella immaculata* and carbaryl (1.12 kg a.i./ha) 3 wk after planting for *Diabrotica* spp. Both plots were sprayed with benomyl (0.56 kg a.i./ha) just prior to bloom initiation to reduce background levels of *B. cinerea* and to suppress a potential white mold problem caused by *Sclerotinia sclerotiorum*.

Plots were irrigated with solid-set overhead sprinklers that applied water at 1.0 cm/hr. Before bloom, both plots were irrigated with 3 cm of water once a week. During and after bloom, frequent evening irrigations were applied to encourage high relative humidity and long leaf wetness duration periods. The early-sown plot received 14 bloom and postbloom evening irrigations that ranged from 0.25 cm to 4 cm, and the late-sown plot received four 2-cm evening irrigations during bloom, followed by 13 days of rain (>0.2 cm/day) after bloom.

**Inoculum production.** Three isolates of *B. cinerea*, selected for their ability to sporulate on Difco potato dextrose agar (PDA) and to grow on PDA containing benomyl (10 mg a.i./L), were chosen from a group of isolates collected from sporulating bean stems in commercial fields earlier in 1981. Benomyl tolerant isolates were used so that inoculum placed in the plots could be distinguished from background levels of *B. cinerea*. The three isolates were grown

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on Difco potato dextrose agar (PDASB) containing streptomycin (100 mg/L) and benomyl (10 mg a.i./L) for 10–14 days under 12 hr of near-ultraviolet and 12 hr of white fluorescent light at room temperature (22 C) until spores formed. Spores were collected by gently washing the plates with sterile distilled water containing Tergitol NP-10 (100 µl/L) (Sigma Chemical Co., St. Louis, MO 63178). The spore suspensions for each isolate were then combined, filtered through two layers of cheesecloth, adjusted to  $10^6$  spores per milliliter, and plated by spreading 1.0 ml of the suspension on 15-cm-diameter petri dishes containing 50 ml of PDASB. The cultures were incubated as described previously for 6–10 days and used as point sources of inoculum.

**Point inoculum sources.** Within each plot, four point sources of inoculum were set out at bloom initiation on a 25-m grid pattern, which was considered adequate to avoid overlapping spread patterns of inoculum. Each point source consisted of four sporulating cultures arranged at ground level in a 30 × 30-cm square. Inoculum sources were exchanged for new inoculum after each irrigation or rainfall, thereby allowing for maximum inoculum dispersal during bloom. Eight inoculum exchanges were made in the early-sown plot and six in the late-sown plot. Inoculum was removed from all point sources at full bloom to determine the effect of primary inoculum sources on continued disease development.

**Spore dispersal.** To measure spore dispersal, conidial populations on plants at several distances from the point sources of inoculum were determined at 5- to 6-day intervals beginning at bloom initiation and continuing until harvest. The plants sampled were located at the corners of a series of squares concentric around the inoculum sources with two sides parallel to the rows. Distances sampled were 127, 254, 383, 637, and 892 cm from the inoculum source. The 892 cm distance was not included in the late-sown plot. On each sampling date, one plant per distance was selected at random with respect to direction from each point source.

After removing the roots and any plant parts showing gray mold symptoms, the sampled plants were weighed and then individually washed by agitating for 30 sec in 500 ml of distilled water containing Tergitol (100 µl/L). Kritzman and Neter's (14) selective medium for *B. cinerea* (SBM) was used to determine the spore concentration on the plants. For this purpose, SBM was modified by deleting  $\text{NaNO}_3$ ,  $\text{K}_2\text{HPO}_4$ ,  $\text{MgSO}_4$ ,  $\text{KCl}$ , and  $\text{CuSO}_4$  and add-

ing Difco PDA (5.0 g/L), streptomycin (100 mg/L), metalaxyl (Ridomil 2EC, 10 µl/L), and benomyl (10 mg a.i./L). A portion of the plant wash was serially diluted and four 0.2-ml samples at two dilutions were spread on the surface of SBM plates. The dilutions chosen depended on previous sampling dates and ranged from 1 : 1 to 1 : 6. After incubation at 22 C for 72 hr, nonsporulating colonies that had typical morphology of *Botrytis* on SBM were counted and the spore population per plant was determined. To verify the identity of *B. cinerea* on SBM, randomly chosen individual colonies were transferred to PDASB. Isolates were positively identified to *B. cinerea* on the basis of conidial formation on PDASB.

#### ***B. cinerea* incidence on blossoms and pod rot disease gradients.**

Incidence of *B. cinerea* on blossoms and of gray mold pod rot was determined at several distances from the point sources of inoculum. The distances measured were located at the midpoints on a series of concentric squares around the inoculum source with two sides parallel to the rows. In the early-sown plot, distances of 90, 271, 451, and 721 cm were measured; and in the late-sown plot, a distance of 180 cm was substituted for the 721 cm distance.

Blossoms were sampled at 50% bloom and full bloom by sampling 10 blossoms at each distance and in each direction from each of the four inoculum sources. The blossoms sampled were all showing initial stages of senescence and were selected randomly over the entire plant. Sampled blossoms were placed in individual containers and later plated individually into 5-cm-diameter petri dishes containing Bacto agar plus streptomycin (100 mg/L) and benomyl (10 mg a.i./L). Incidence of *B. cinerea* on blossoms was determined after incubating the plates for 8–10 days under 12 hr of near-ultraviolet and 12 hr of white fluorescent light at 22 C and then examining the blossoms for sporulation of the fungus.

At harvest, three plants per distance were sampled in each direction from each point source. The percent pod rot for each three-plant sample was determined by examining all pods over 10 cm in length. Fifty to 70 pods comprised each three-plant sample.

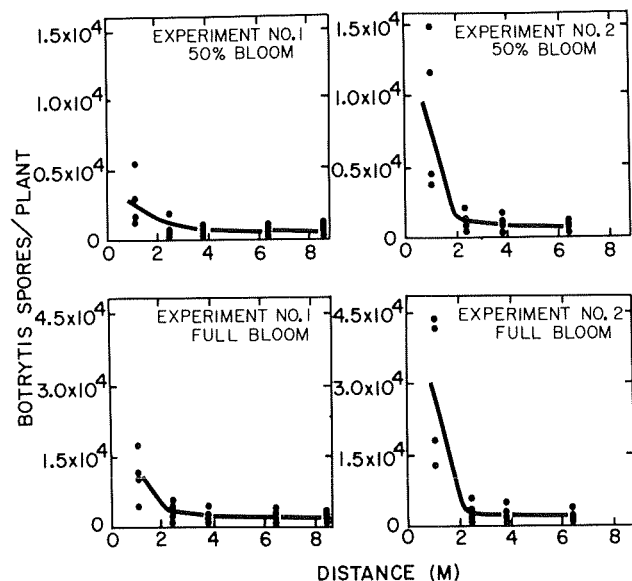
## RESULTS

**Spore dispersal.** During bloom, when point sources were present in the field, plant spore populations were highest within 127 cm from the source and decreased rapidly as distance increased from the source (Fig. 1A-D). At 127 cm, populations averaged greater than  $2 \times 10^3$  spores per plant at 50% bloom and  $10^4$  spores per plant at full bloom. Few spores, ie, <100 spores per plant, were detected beyond 254 cm.

After removal of the point inoculum sources at full bloom, spore populations per plant continued to increase at all distances during the pod filling stages (Fig. 2A-F). Production of inoculum from secondary foci, mainly on colonized senescent blossoms lying on the soil surface, was visible within the experimental plots. Even though the spore populations per plant reached very high levels after bloom, the location of the point inoculum source in both plots was discernable at harvest. At 127 cm from the inoculum source, spore populations per plant at harvest represented a 20- and 30-fold increase over the full bloom populations in the early and late-sown plots, respectively.

***B. cinerea* incidence on blossoms and pod rot incidence.** The mean incidence of *B. cinerea* on blossoms at increasing distance from the point inoculum source (Fig. 3A and B) resembled the per plant spore population curves for similar sampling dates (Fig. 1). The relative variance around the means of *B. cinerea* incidence on blossoms, especially at distances greater than 127 cm, was larger than in the spore population curves. In both plots, the average incidence of *B. cinerea* on blossoms at 50% bloom was greater than 52% at the 90-cm distance but less than 20% at distances beyond 254 cm. At full bloom, a similar relationship was observed, although the overall incidence of *B. cinerea* on blossoms was greater at all distances measured.

The location of the point inoculum source was clearly evident from the pod rot incidence data (Fig. 4A and B). In the early-sown plot, pod rot incidence averaged 2% at 90 cm from the inoculum source but decreased to less than 0.2% at distances greater than 271



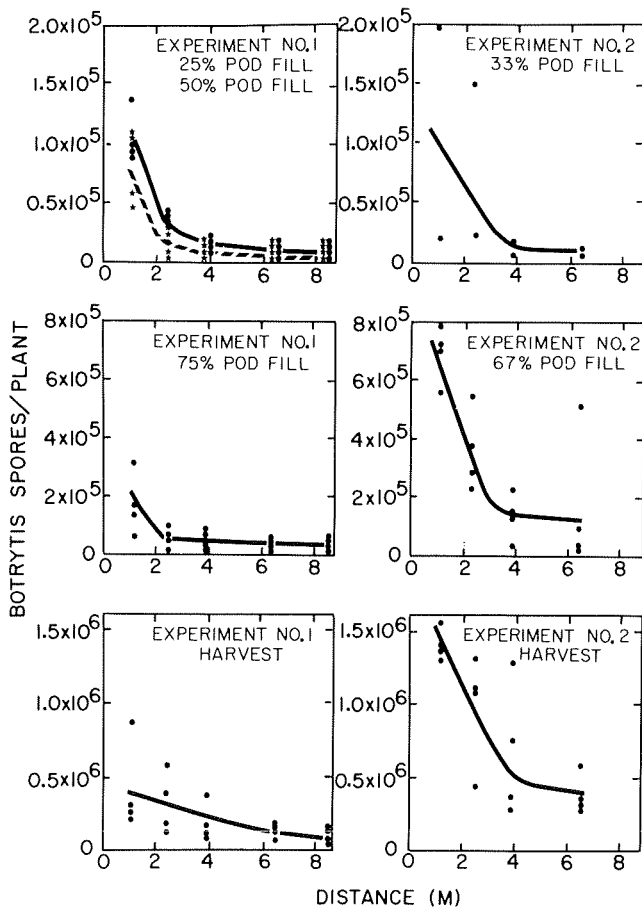
**Fig. 1.** Spore populations of *Botrytis cinerea* on bean plants during bloom at various distances from the inoculum source. **A and B.** 50% bloom, experiment 1 and 2, respectively. **C and D.** full bloom, experiment 1 and 2, respectively. Each point represents the average of four dilution plates per plant, and the curves are drawn through the mean spore population at each distance from the inoculum source. Experiment 1, early-sown plot; experiment 2, late-sown plot.

cm. Similarly, in the late-sown plot, pod rot averaged 7% at 90 cm from the inoculum source but only 2.5% at a distance of 451 cm.

**Analysis of spore dispersal and disease gradients.** Spore dispersal and disease incidence gradients were analyzed by regression of log Y on log X where Y equals the plant spore population or disease incidence at distance X. The data for spore populations per plant were transformed to spore populations per gram of plant tissue to reduce the variation in plant size within sampling dates and to standardize the size of the spore trap throughout the study. The assumption was made that the plant surface area to weight relationship remained proportional throughout crop development.

Plant foliage spore populations at 50% bloom at distances of 625 and 889 cm from the inoculum source and the 889 cm spore population per plant at full bloom were not included in the log-log analysis because these populations were no longer decreasing over distance and were not significantly greater than zero. Inclusion in the analysis would have artificially flattened the gradients (5). Likewise, pod rot incidence data in the early-sown plot at distances of 451 cm and 721 cm from the inoculum source were excluded.

Slopes of log-log spore dispersal gradients (Fig. 5A and B) showed significant flattening from 50% bloom to harvest ( $P = 0.05$ ). Gradients at harvest were also significantly flatter than full bloom gradients at  $P = 0.05$  and  $P = 0.08$  in early and late-sown plots, respectively. The increase in spore populations per gram of plant over time is evident from the progressive increase in height of the gradients. Both the increasing spore populations after full bloom and flattening of the gradients are evidence for production of secondary inoculum.

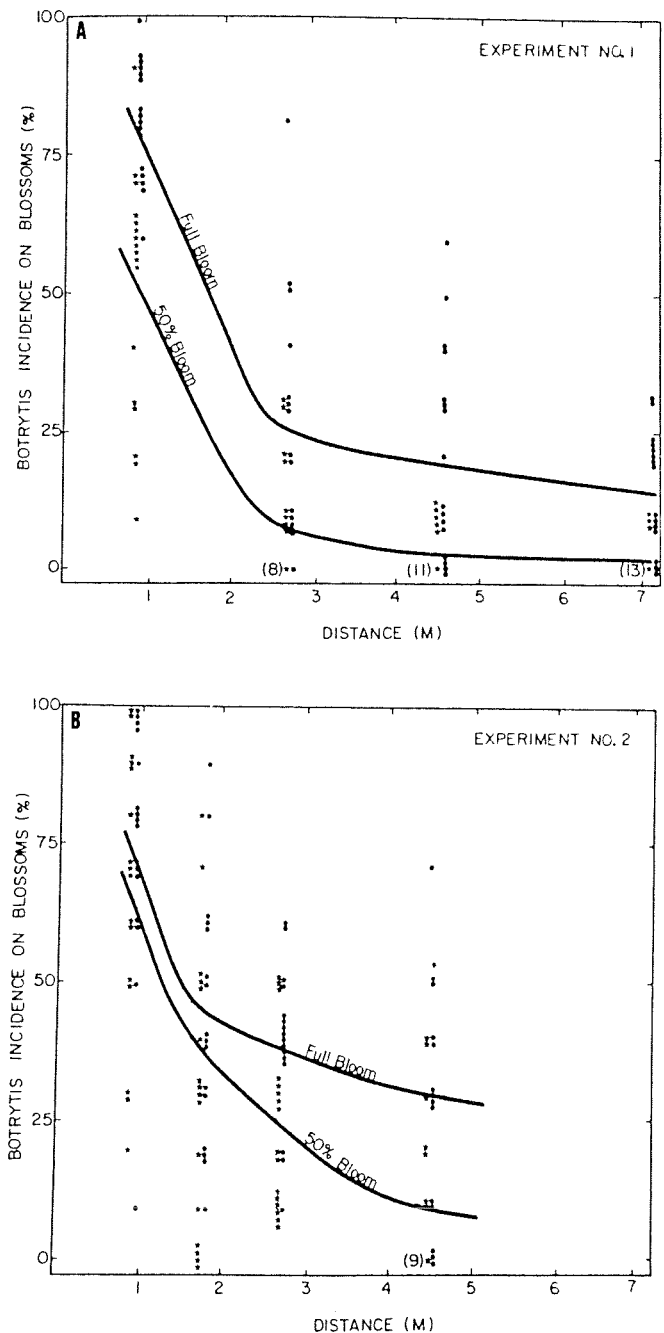


**Fig. 2.** Spore populations of *Botrytis cinerea* on bean plants during pod fill at various distances from an inoculum source which was removed at full bloom. **A**, 25 and 50% pod fill, experiment 1. **B**, 33% pod fill, experiment 2. **C**, 75% pod fill, experiment 1. **D**, 67% pod fill, experiment 2. **E and F**, harvest, experiments 1 and 2, respectively. Each point represents the average of four dilution plates per plant, and the curves are drawn through the mean spore population at each distance from the inoculum source. Experiment 1, early-sown plot; experiment 2, late-sown plot.

The incidence of pod rot was significantly lower ( $P = 0.01$ ) than the incidence of *B. cinerea* on blossoms (Fig. 6A and B). The slopes of the blossom incidence gradients flattened from 50% bloom to full bloom; however, blossom incidence at full bloom compared to pod rot at harvest did not significantly flatten ( $P = 0.34$  and  $P = 0.81$ , early and late-sown plots, respectively).

## DISCUSSION

The use of benomyl-resistant isolates of *B. cinerea* permitted the study of dispersal and disease gradients with minimal background contamination from natural benomyl-sensitive populations. In 1980, benomyl-resistant isolates were not detected at the OSU



**Fig. 3.** Incidence of *Botrytis cinerea* on blossoms at 50% and full bloom at various distances from the inoculum source. Each point (stars, 50% bloom and dots, full bloom) represents the average for 10 blossoms, and the curves are drawn through the mean incidence at each distance. **A and B**, experiment 1 (early-sown plot) and experiment 2 (late-sown plot), respectively.

Vegetable Research Farm (*unpublished*), but, because benomyl-resistant strains of *B. cinerea* are widespread in commercial snap bean fields in the Willamette Valley, some of the spores detected on the bean plants may not have originated from the point inoculum source. Nevertheless, the dispersal and disease gradients were evidence for the influence of within-field inoculum sources on disease development. These results are supported by studies of tomato plantings which demonstrated that disease incidence of *B. cinerea* was limited to within 8 m of a line inoculum source (3).

Spore populations on bean foliage and incidence of pod rot were significantly lower in the early-sown plot than on plants at similar stages of growth in the late-sown plot. These differences may be due, in part, to irrigation schedules and/or other environmental conditions. The early-sown plot was irrigated more frequently than the second, and the frequent irrigations may have removed a

significant number of spores from the foliage. This has been observed in studies of Botrytis blight of macadamia racemes; heavy rains suppressed disease by removing spores from the plants (7). Also, the duration of irrigations was shorter in the early-sown plot than in the late-sown plot, and hence, prolonged high-moisture conditions required for germination, growth, infection, and sporulation of *B. cinerea* may not have been present (9). In addition, weather conditions after full bloom and during pod fill were warm (daily mean temperature = 17.1 C) and dry (mean precipitation = 0.4mm/day) contrasted with cool (daily mean temperature = 12.6 C) and wet (mean precipitation = 6.8 mm/day) conditions in the late-sown plot; hence, the warm, dry conditions may not have been conducive for disease development (2).

Jarvis (8) reported that conidia of *B. cinerea* can be dispersed either as dry spores on air shock waves and turbulent currents or as splash-dispersed composite projectiles of dry conidia coating the surface of water droplets. Stedman (18), studying dry and splash

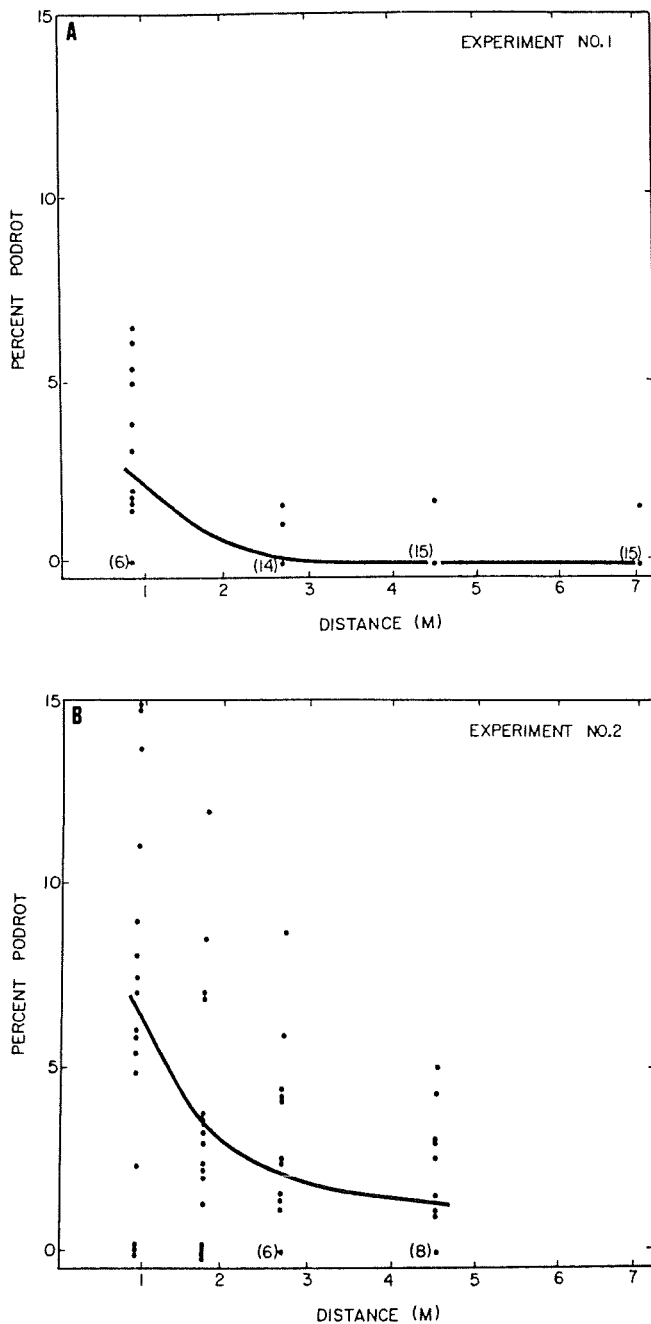


Fig. 4. Gray mold pod rot incidence on snap bean at harvest at various distances from a *Botrytis cinerea* inoculum source. Each point represents the average of 50-70 pod disease readings and the curves are drawn through the mean incidence at each distance. **A and B**, experiment 1 (early-sown plot) and experiment 2 (late-sown plot), respectively.

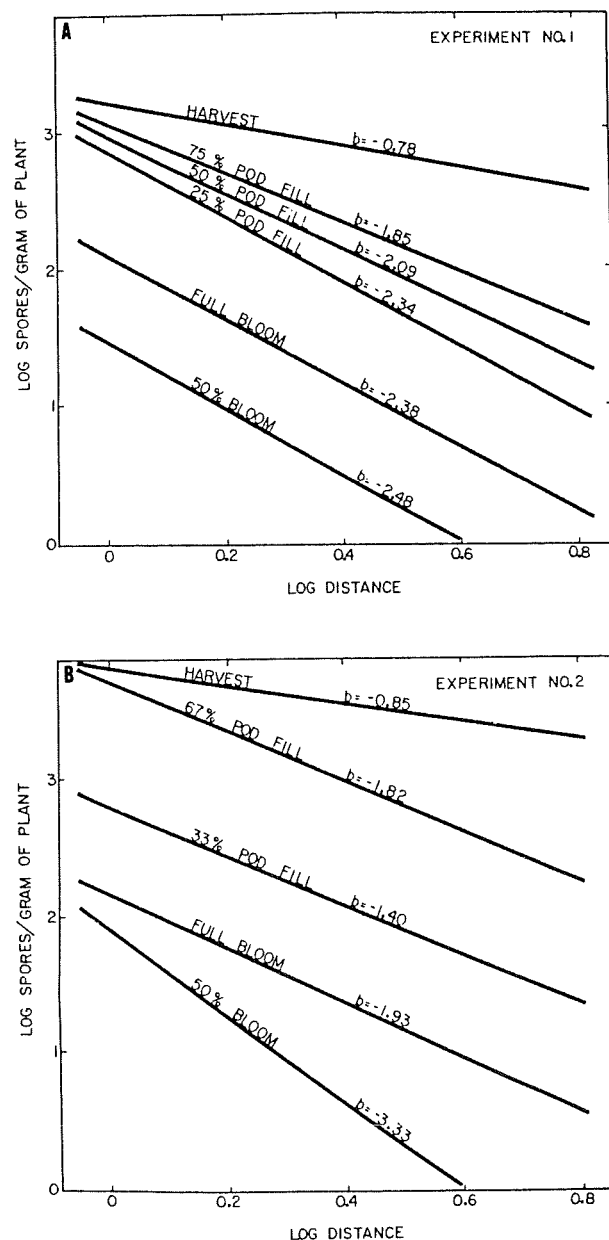


Fig. 5. Log plant spore populations versus log distance from the point inoculum source from 50% bloom until harvest. Values of 'b' indicate the slope of the regression of log spores on log distance. Standard errors of the slopes ranged from 0.81 at 50% bloom to 0.37 at harvest. **A and B**, experiment 1 (early-sown plot) and experiment 2 (late-sown plot), respectively.

dispersal of *Lycopodium clavatum* spores from point sources in field beans (*Vicia faba* L.), suggested that his results may simulate dispersal of *B. cinerea* spores. Slopes of the log-log transformed dispersal gradients of *L. clavatum* trapped on cylinders were  $b = -1.65$  and  $-3.59$  for dry and splash dispersed spores, respectively. In our study, inoculum was changed following each irrigation, and spore dispersal during bloom from the point inoculum sources represented the primary dispersal gradient. Slopes of these gradients at 50% and full bloom ranged from  $-3.33$  to  $-1.93$ , and were intermediate to slopes obtained by Stedman (18) for splash and dry dispersal. Our data suggest that *B. cinerea* spores were dispersed by both mechanisms.

Production of inoculum from secondary foci (ie, colonized senescent blossoms lying on the soil surface) was visible within the plots after full bloom. After removal of the point inoculum source, increases observed in plant spore populations may have originated from these secondary foci or from sources outside the field. Because the spore dispersal gradients were maintained during the 20- to 30-fold increase of postbloom plant spore populations (Fig. 2), the secondary inoculum probably originated from within the field. The observed flattening of the log-log spore dispersal gradients was expected due to production of secondary inoculum (5).

Under field conditions, favorable environmental conditions coupled with high spore populations on the foliage does not ensure the development of gray mold. For infection of healthy tissue to occur, an exogenous energy source, such as senescent blossoms, must be present at the infection court (2,9). Van den Heuvel (19) demonstrated this by inoculating bean foliage with water or glucose and phosphate-amended conidial suspensions of *B. cinerea*. The suspension containing glucose and phosphate, both readily available compounds in senescent blossoms (19), resulted in spreading gray mold lesions; whereas the conidial suspensions in water alone resulted in only a few necrotic flecks. Thus, senescing blossoms, which are readily infected by conidia of *B. cinerea* (13), provide both the primary means for infection of pods and for the production of secondary inoculum. Gradients, therefore, were measured for *B. cinerea* on blossoms to determine the influence of a point inoculum source on the initiation of pod rot. Furthermore, because secondary inoculum was produced and dispersed after full bloom, comparisons of the slope of the blossom incidence gradient with the slope of the pod rot disease gradient should provide a basis for making inferences on the role of primary and secondary inoculum on disease spread.

Gradients of *B. cinerea* incidence on blossoms were measurable at 50% and full bloom. A larger percentage of the blossoms at full bloom had *B. cinerea* associated with them than those at 50% bloom. This was expected because of the increased length of exposure of the blossoms (1 wk) to the initial inoculum. Also, the flattening of the gradients between 50% and full bloom may be due partly to multiple infection of blossoms near the source. Use of the multiple infection transformation could minimize the differences between gradients (5); however, because the importance of multiple conidia on blossoms and relative to pod rot development was not determined, the gradients were left untransformed.

Comparisons of gradients for incidence of *B. cinerea* on blossoms at full bloom with amount of pod rot illustrate two important points. First, the low percentage of pod rot compared to the high percentage of *B. cinerea* on blossoms demonstrated that infection of pods from blossom inoculum was an infrequent event. Second, the slopes of the pod rot gradients at harvest did not significantly flatten compared with those for the blossom data at full bloom. This observation is in contrast to the spore dispersal gradients, which, due to production of secondary inoculum, showed significant flattening between full bloom and harvest. Because production of secondary inoculum was not observed until after full bloom, only inoculum from the point inoculum source was available for blossom infection during bloom. Thus, the nonsignificant flattening of the pod rot gradients suggests that primary inoculum, which infects the blossoms during bloom, may be more important in pod rot development than the secondary inoculum produced after bloom.

Rowe and Powelson (17), studying disease gradients of *Cercospora* foot rot, concluded that epidemic levels of foot rot were dependent on primary inoculum which was produced on infected wheat stubble from previous crops. Secondary inoculum, produced at low levels on infected plants, occurred too late in crop development to be important in disease development. In this study, a comparison of disease and dispersal gradients suggested that primary inoculum was more important in disease development even though large amounts of secondary inoculum were produced.

The importance of primary inoculum of *B. cinerea* in utilization of blossoms as a food base may involve biological competition for the senescent blossom tissue with other saprophytic organisms (1). *B. cinerea*, a weak parasite, has a competitive advantage in the infection and colonization of the blossom tissue only if the inoculum arrives during bloom. If inoculum arrival is delayed, as in the case of secondary inoculum, other organisms could colonize the

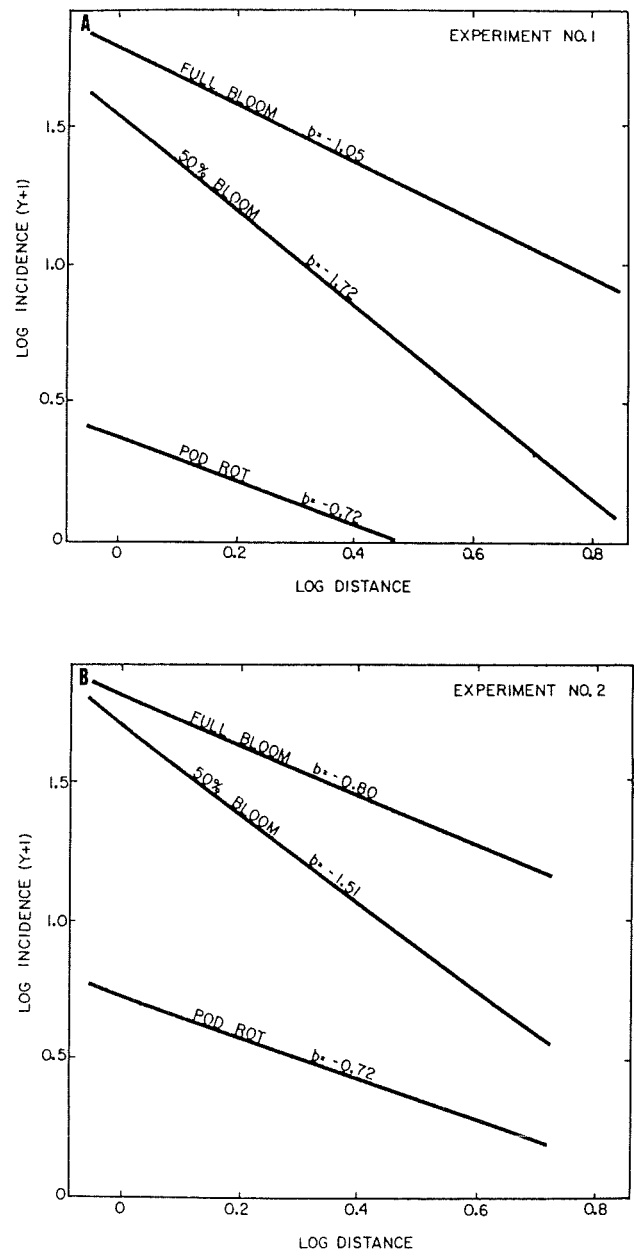


Fig. 6. Log disease incidence versus log distance from the point inoculum source for blossom incidence at 50% and full bloom and pod rot incidence at harvest. Values of "b" indicate the slope of the regression of log incidence on log distance. Standard errors of the slopes ranged from 0.36 at 50% bloom to 0.21 for pod rot. A and B, experiment 1 (early-sown plot) and experiment 2 (late-sown plot), respectively.

senescent blossom and make the blossom tissue unavailable to *B. cinerea*. Sampled blossoms at 50% and full bloom were frequently colonized by other fungi along with *B. cinerea*, and on blossoms with no detectable *B. cinerea*, other fungi were always isolated. Additional indirect evidence for biological competition for senescent blossom tissue in snap beans was observed in studies in which benomyl-resistant strains of *B. cinerea* were present in benomyl spray trials (10). When benomyl was sprayed on blossoms, a significantly higher incidence of gray mold resulted when compared with the untreated controls. Johnson (10) suggested that reduced competition occurred between *B. cinerea* and other fungi (sensitive to benomyl) for the blossom tissue.

Identification and quantification of local inoculum sources within growers' fields may explain some of the variation in the amount of pod rot observed. In addition, the time of blossom infection and colonization by *B. cinerea* and the role of other biological organisms in competition for this food base as it relates to disease development needs further investigation.

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