Density and Spatial Pattern of Propagules of *Macrophomina phaseolina* in Corn Rhizospheres

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Paper 11954 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh 27695-7643.
The use of trade names in this publication does not imply endorsement by the North Carolina Agricultural Research Service of the products named nor criticism of similar ones not mentioned.
We thank Joe Powell and Jerry and Bryan Weaver for their cooperation in this study and sincerely appreciate the excellent assistance provided by Charles R. Harper.
Accepted for publication 17 June 1989 (submitted for electronic processing).

ABSTRACT

Olanya, O. M., and Campbell, C. L. 1989. Density and spatial pattern of propagules of *Macrophomina phaseolina* in corn rhizospheres. Phytopathology 79:1119-1123.

Propagule density of *Macrophomina phaseolina* in soil was monitored from May to September 1985 at a total of eight sites chosen to represent a range of propagule densities in two fields. Corn seedlings were removed from one of two adjacent plots of 25 contiguous quadrats at each site to give reduced root density. Propagule density did not vary significantly within a plot or between adjacent plots through the season. From a regression of Lloyd's index of mean crowding ($\mathring{x}$) on mean propagule density, individual propagules, i.e., colony-forming units of microsclerotia, were the basic unit of contagion in eight of 10 cases and these colony-forming units had a random spatial pattern. Monthly values of Morisita's index of aggregation ranged from 1.06 to 1.15 in Field A (Edgecombe County) and from 1.12 to 2.17 in Field B (Wayne County), confirming a random or slightly aggregated pattern of propagules. For frequency count data of propagule density, the Poisson distribution was appropriate in 18 of 40 and 20 of 40 cases for location A and B, respectively; however, the negative binomial distribution did not describe any data set. Because density and spatial pattern of propagules of *M. phaseolina* were generally similar throughout the growing season, this suggests either a lack of detectable reproductive activity and decay of propagules in soil during periods of active corn root growth or equal rates of propagule reproduction and death.

The microbiological equilibrium of soil varies due to the influence of edaphic, climatic, and weather factors; however, the greatest changes are caused by plant root growth (20). The developing rhizosphere strongly influences nutrient availability and biological interactions at the root/soil interface. To date, emphasis in spatial pattern analysis of soilborne pathogens has been placed primarily on the effect of edaphic factors (11,15-18). Wollum and Cassel (22), however, investigated the spatial variability of *Rhizobium japonicum* Buchanan in two soils and suggested that root densities, as well as inherent soil properties, seasonality, and management practices contributed to changes observed in rhizobia populations.

Macrophomina phaseolina (Tassi.) Goid causes charcoal rot of more than 250 species of plants (6). The fungus survives in soil primarily as microsclerotia that are formed in the host tissues and released into the soil as tissues decay (4,6). Viable microsclerotia can persist in soils for at least 3 mo (10).

Initial progress has been made in describing the spatial pattern of propagules of *M. phaseolina* with quadrat sizes of 6 × 6 m (2), 1.02 × 0.3 m (15) or 1 × 1 m (18). In these studies, propagules of this fungus have been found to be spatially aggregated (2,15,18). The question of spatial variability of propagules in smaller areas, specifically in the host rhizosphere, remains.

The population dynamics of *M. phaseolina* have been studied in natural soils under the influence of *Euphorbia lathyris* L. (gopher plants) (23), *Helianthus annuus* L. (sunflower) (14), and *Glycine max* L. (soybean) (19) and in amended soils (8). With the exception of a few cases, determination of propagule density has been limited largely to pre- and post-growing season samples. As a result, little information is available about the temporal dynamics of propagules of *M. phaseolina* during a growing season under standard cultural conditions. The objective of this study, therefore, was to examine the population dynamics and spatial pattern of *M. phaseolina* in relatively small areas during a growing season.

MATERIALS AND METHODS

Site description. A preliminary survey of fields in two North Carolina counties (Edgecombe and Wayne), indicated population levels of *M. phaseolina* varied in naturally infested soils. One field from each county was selected for further study, using the presence of a corn crop and range of inoculum density as selection criteria. In Field A (Edgecombe County), the soil was a loamy sand (fine, loamy, mixed thermic, and typic hapludult) with a mean composition from eight samples of 64.4% sand, 30.4% silt, and 6.2% clay. Humic matter ranged from 0.1-0.5 g/100 cm^3 of soil and pH ranged from 5.5 to 6.0. Preliminary spring assays indicated a range in population range for *M. phaseolina* from 19 to 100 propagules per 10 g of air-dry soil. The field had been cropped to corn in 1983, cotton in 1984, and corn was planted with a row spacing of 90 cm and an approximate density of 6 plants/m row in April 1985.

In Field B (Wayne County), the soil was sandy loam or a loamy sand (fine, loamy, silaceous, thermic, typic paleudults) with a mean composition from seven samples of 90.4% sand, 6.4% silt, and 3.2% clay. Humic matter ranged from 0.1 to 0.4 9/100 cm^3 of soil and pH ranged from 4.8 to 5.7. Preliminary assays indicated a population range for *M. phaseolina* of 6-55 propagules/10 g of air-dry soil. The field had been planted with corn in 1983, tobacco in 1984, and corn was planted with a row spacing of 76 cm and an approximate density of 6 plants/m row in April 1985.

Variability of propagule density within a quadrat. To determine the variability of propagule density of *M. phaseolina* within relatively small quadrats, a preliminary study was conducted in each field near the actual plots. In Field A, eight arbitrarily located, 18- × 18-cm quadrats were demarcated and four soil cores (2.5 cm diameter, 6 cm deep) were obtained and assayed individually (3) from each quadrat. In Field B, four arbitrarily located 15- × 15-cm quadrats in each of two sections of a field (separated by an unpaved road) were chosen and nine soil cores were obtained and assayed individually (3) from each quadrat. Coefficient of variation values and variance components within and among

quadrats were calculated from an analysis of variance for each field and compared to ascertain variability within and among blocks and optimum number of soil samples to assay per quadrat (3).

Plot establishment and sampling. In May 1985, four pairs of adjacent plots (= grids of contiguous quadrats) were established at each location. In Field A, row spacing was 90 cm, thus a 90- × 90-cm area containing 25 contiguous quadrats (18 × 18 cm) was established (Fig. 1) on a row containing five to six corn (*Zea mays* L.) plants (~15 cm height) with the corn row at the center of the plot. This plot was designated the normal root density plot. An adjacent plot was established with the same dimensions and the same number of contiguous quadrats, but corn plants were uprooted and removed manually. This adjacent plot was designated the reduced root density plot. Corn was chosen as a crop plant both for its importance as a potential host for *M. phaseolina* and for convenience; however, no attempt was made to measure actual root densities in soil. For Field B, with a row spacing of 76 cm, plots (= grids of contiguous quadrats) were established (Fig. 1) similarly in May 1985, with the exception that each plot of 25 contiguous quadrats (15.2 × 15.2 cm) had an area of 76 × 76 cm.

Sampling was conducted at approximately monthly intervals from May to September. A single soil core (2.5 cm diameter, 6 cm deep) was obtained from each quadrat. Within each quadrat, a different area (~3 cm diameter) was sampled on each subsequent sampling date. No area within a quadrat was sampled more than once during the study. Soil was transported to the laboratory, air dried, and assayed for *M. phaseolina* (3). Soil moisture was determined gravimetrically at each sample date (5).

Data analysis. To ascertain whether propagule density varied with treatment or time, an analysis of variance for a split-plot design was conducted for data from each field. Normal or reduced corn-root densities were considered as whole plots, sample times (May, June, etc.) as subplots, and quadrats as samples within the four replicate plots per field. Significance of effects was determined by appropriate *F*-tests.

Morisita's index was calculated (7) to give a measure of the degree of aggregation of propagules of *M. phaseolina*. The variance and the mean for each plot were computed using the Univariate procedure of the Statistical Analysis System (21).

Lloyd's index of mean crowding, $\overset{*}{x}$ was calculated from mated variance (s^2) and mean ($\bar{x}$) values at each plot-time combination such that $\overset{*}{x} = \bar{x} + (s^2/\bar{x}) - 1$. The method of Iwao (12,13) was used to determine the index of basic contagion (b_0) (i.e., mean crowding of individuals) and the density-contagiousness coefficients (b_1) (i.e., patchiness of clusters) from the regression model:

$$\overset{*}{x} = b_0 + b_1\bar{x}.$$

The value of b_0 is related to size of colonies or clumps of individuals that constitute the basic unit of the spatial pattern. If $b_0 = 0$, an individual is the basic unit of spatial pattern and when $b_0 > 0$ or < 0, there is a positive or negative association, respectively, between individuals. In the case of *M. phaseolina*, a colony-forming unit composed of a single microsclerotium or several microsclerotia as detected in the selective assay (3), would represent an individual. The value of b_1 indicates the "manner in which individuals or groups of individuals (clusters) distribute themselves in their habitat with changing mean density" (12), such that when $b_1 > 1$, there is aggregation of the basic units, when $b_1 = 1$, there is a random pattern, and when $b_1 < 1$ there is a regular pattern.

Five frequency distributions (negative binomial, Neyman type A, Poisson, positive binomial, and Thomas double poisson) were examined for goodness-of-fit to propagule density, frequency count data. The propagule counts were arranged into a frequency table with five class intervals. The class interval was calculated by dividing the range between the highest and lowest inoculum counts into five equal parts by fields, sites, and over the 5-mo period. Distribution fitting was conducted using a FORTRAN program (9). A chi-square, goodness-of-fit test was then applied to the observed and expected frequency distributions to determine if the observed data differed significantly from the fitted probability distribution. A $P \geq 0.05$ indicated that the sample data did not differ significantly from the tested distribution.

RESULTS

Variability of inoculum density within a quadrat. At both locations, the coefficient of variation for propagule density was generally low. Mean coefficient of variation values were 29% (range 10–45%), 47% (range 18–71%), and 23% (range 15–30%) for Field A, Field B, section 1, and Field B, section 2, respectively. In Field B, section 1, the CV value of 71% was associated with the lowest propagule density ($\bar{x}$ = 2.6 propagules/10 g of dry soil). If this one value was excluded, mean CV value for Field B, section 1 was 39% (range 18–52%). Propagule density of *M. phaseolina* did not differ for Field A and Field B, section 2, but significant differences in propagule density among grids of quadrats were found for Field B, section 1. The ratio of variance components for samples within grids (σ^2) to among grids (σ_G^2) was 0.77 for Field B, section 1, and 2.55 for Field B, section 2 (Table 1). Thus, with a high cost of assay per sample ($1.89) relative to the cost to select a sample ($0.10), the optimum number of samples to take per quadrat for both sections in Field B was one (3). It was not possible to calculate the ratio of the variance components for Field A because of the relatively higher error variance and lower variation among blocks (Table 1); however, for convenience, one sample per quadrat was also taken at this location at each date.

Temporal variation in propagule density. Mean propagule densities of *M. phaseolina* differed between the two locations. Representative maps of mean propagule density of *M. phaseolina* for one pair of adjacent plots in each field are presented in Figure 1. In Field A, the mean density over all plots ranged from 45.7–49.7 propagules/10 g of air dry soil (Fig. 2), while in Field B, it ranged from 19.5–27.0 propagules/10 g of air-dry soil (Fig. 2). From the overall analysis of variance (Table 2), no differences

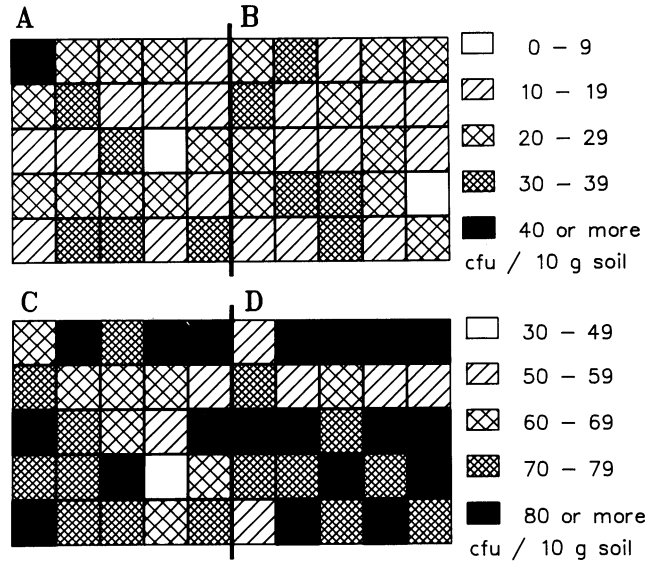

Fig. 1. Propagule density (colony-forming units (cfu)/10 g of air dry-soil) of *Macrophomina phaseolina* in 50 quadrats from one of four pairs of adjacent plots in each of two fields. **A and B,** In Field B (Wayne County) each plot consisted of 25 15- × 15-cm quadrats. On 6 June 1985, values for mean cfu/10 g of soil and Morisita's index were 21.6 and 1.11, respectively, in plot **A** (corn removed) and 23.5 and 1.14 in Plot **B** (corn present). **C and D,** In Field A (Edgecombe Couty) each plot consisted of 25 18- × 18-cm quadrats. On 8 August 1985, values for mean cfu/10 g of soil and Morisita's index were 71.8 and 1.03, respectively, in plot C (corn removed) and 80.2 and 1.01, respectively, in plot D (corn present).

($P = 0.05$) between the plots with normal or reduced corn root density or among sample times were observed. For example, at the beginning of the experiment (May) in Field B, an average of 24 and 22 microsclerotia per 10 g of air-dry soil in the two treatments, respectively, were obtained and remained relatively uniform through June, July, and August with a mean of 29 and 25 microsclerotia/10 g of air-dry soil, respectively, in the September sample.

Variation in spatial pattern of propagules. For Field A, values of Morisita's index ranged from 1.06 to 1.15 (Fig. 3), but did not differ significantly from 1.00, indicating a random pattern of the propagules. For Field B, values of Morisita's index ranged from 1.12 to 2.17 and were greater than 1.00 ($P = 0.05$) in May and August. In these two months, significant aggregation was indicated in all plots.

From the regression of Lloyd's index of mean crowding on the mean propagule density, individuals or, in this case, colony-forming units of microsclerotia of *M. phaseolina* were the basic components of the spatial patterns. Values of b_0 were not different ($P = 0.05$) from zero at three and five of five sample dates for locations A and B, respectively (Table 3). Values of b_1 were not different ($P = 0.05$) from one at any sample date for location A or B (Table 3), indicating that individual colony-forming units of *M. phaseolina* had a random spatial pattern.

The random or near random pattern of propagules for many plot-sample time combinations was confirmed by the fact that among the models tested, only the Poisson was appropriate for describing any of the data sets. Data from 10 of 20 normal corn root density–plot-sample time combinations and 8 of 20 with reduced corn root density were described by the Poisson for Field A. Whereas for Field B, 10 of 20 plot-sample time data sets in each treatment were described by a Poisson distribution.

TABLE 1. Analysis of variance for propagule density of colonies of *Macrophomina phaseolina* in eight grids of contiguous quadrats in each of two fields and ratio of variation within grids (σ^2) to variation among (σ_g^2) grids[a]

Location	Source	df	Mean squares	Expectation of mean squares
Field A (Edgecombe County)				
Section 1	Grids	7	201.79	$\sigma^2 + 4\,\sigma_g^2$
	Error	24	340.56	σ^2
Field B (Wayne County)				
Section 1	Grids	3	194.10	$\sigma^2 + 9\,\sigma_g^2$
	Error	32	11.88	σ^2
Section 2	Grids	3	460.10	$\sigma^2 + 9\,\sigma_g^2$
	Error	32	193.15	σ^2

[a]In Field A, four samples were assayed per quadrat; in Field B, nine samples were assayed per quadrat.

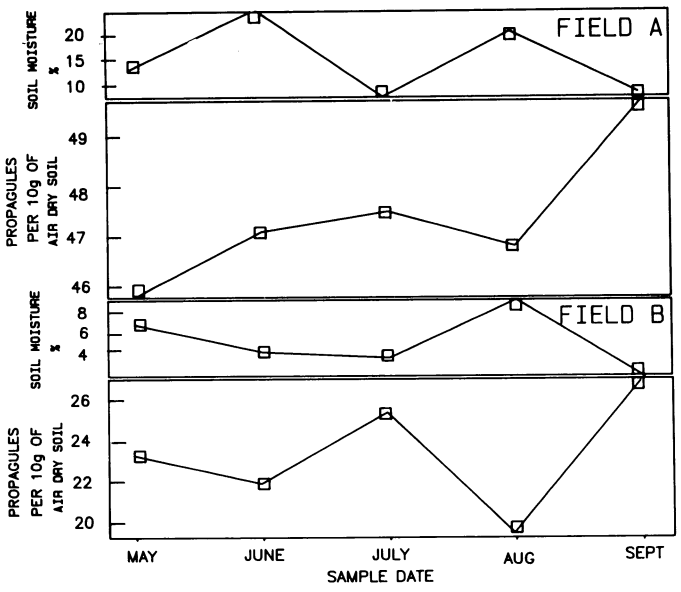

Fig. 2. Mean propagule density of *Macrophomina phaseolina* and percent soil moisture in grids of contiguous quadrats from May to September in Fields A and B (Edgecombe and Wayne counties, respectively).

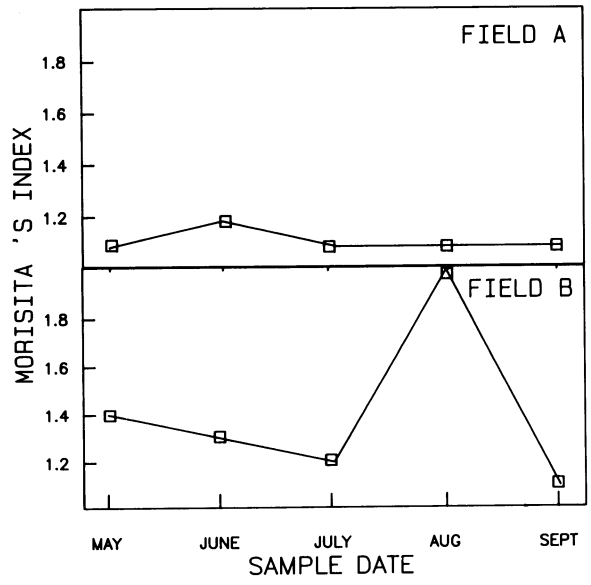

Fig. 3. Mean value of Morisita's index of aggregation at five sample dates for populations of *Macrophomina phaseolina* for Fields A (Edgecombe County) and B (Wayne County) from grids of contiguous quadrats.

TABLE 2. Analysis of variance for propagule density of samples of *Macrophomina phaseolina* from four pairs of adjacent plots of 25 contiguous quadrats with and without the presence of corn plants in each of two fields from May to September 1985

	Field A			Field B		
Source	df	Sum of squares	Probability of a greater F value	df	Sum of squares	Probability of a greater F value
Replications[w]	3	291,371	0.001 *	3	276,984	0.001 *
Treatment[x]	1	3,101	0.193 NS	1	3,478	0.434 NS
Rep*Trt	3	3,331	0.001 *	3	12,879	0.001 *
Samp(Rep*Trt)[y]	192	44,444	0.081 NS	192	31,988	0.187 NS
Time	4	1,718	0.760 NS	4	6,902	0.337 NS
Rep*Time[z]	12	11,079	0.001 *	12	16,394	0.001 *
Trt*Time	4	2,286	0.337 NS	4	2,307	0.725 NS
Rep*Trt*Time[z]	12	5,424	0.008	12	13,386	0.001 *

[w]Each pair of adjacent plots (= grids of contiguous quadrats) was considered a replication for convenience, the presence or absence of corn plants was designated as treatment.
[x]Samp (Rep*Trt) = samples within (Rep*Trt).
[y]The Rep*Trt mean square was used as the error term for the treatment main effect.
[z]The error term for main effect of time was the mean square of (Rep*Time + Rep*Trt*Time).

DISCUSSION

The temporal and spatial dynamics of a population of a soilborne pathogen can significantly influence conclusions reached in ecological, epidemiological, and management investigations. Although the population dynamics of *M. phaseolina* have been studied extensively, determinations of propagule density and spatial pattern have been limited primarily to pre- and post-growing season samples. In this study, we examined propagule density and spatial pattern exclusively during the growing season in the presence and absence of actively growing host plants.

Within areas of 90 × 90 cm or 76 × 76 cm, the population level of *M. phaseolina* did not vary significantly over time and had a random or nearly random spatial pattern throughout a 5-mo period at two separate locations. Population levels also were similar in soils with corn plants present or removed. Thus, this fungus exhibited either a minimal level of production and release of microsclerotia into soil coupled with near constant levels of propagule survival or equal rates of propagule reproduction and death. Because propagules of *M. phaseolina* can survive at least 3 mo in soil (10) and micosclerotia are generally produced in host tissue (4), the first explanation seems more reasonable. The concept of a virtual lack of reproductive activity for *M. phaseolina* in soil during a growing season was reported by Young and Alcorn (23). When microsclerotial populations of *M. phaseolina* were monitored from February 1981 to January 1982 during the growth period of gopher plant (23), number of viable scierotia per gram of soil generally remained low and constant, and sclerotial numbers increased only after the plant residues were plowed into soil in October.

The basic units of the spatial pattern of *M. phaseolina* in corn rhizospheres were individual, colony-forming units of microsclerotia. This index of contagion (i.e., mean crowding of individuals) has not been determined for other sclerotial fungi. Our finding differs, however, from the results obtained by Belair and Boivin (1) for root knot of carrot, caused by *Meloidogyne hapla*, where aggregates or clusters of individual nematodes were the basic unit of contagion. These nematodes hatch from eggs aggregated in an egg mass (1) and, being obligate parasites, will be likely to cluster at an available, nearby food source after hatching. This behavior probably accounts for the aggregate of individuals being the basic unit of contagion. With *M. phaseolina*, however, individual microsclerotia or small aggregates of microsclerotia that act as a single colony-forming unit in a selective assay are formed in host tissue and are released into soil as host tissues decay. Also, the fact the *M. phaseolina* is not an obligate parasite (6) would remove the necessity for active aggregation at host sites. Thus, the individual microsclerotium or, at least, what appears as an individual in a selective assay is a biologically reasonable basic unit of contagion.

TABLE 3. Parameter estimates (b_0, b_1), standard errors (S_{b_0}, S_{b_1}) for the y-axis intercept and slope and coefficient of determination (R^2) from the regression of Lloyd's index of mean crowding on mean propagule density of *Macrophomina phaseolina*

Location/ date	Regression estimates				
	b_0	S_{b_0}	b_1	S_{b_1}	R^2
Field A					
May	3.51	3.312	0.98	0.0067	0.99
Jun	7.61*[z]	1.003	0.97	0.020	0.99
Jul	−0.26	2.627	1.07	0.052	0.99
Aug	9.41	3.416	0.88	0.068	0.98
Sep	5.56*	0.958	0.94	0.018	0.99
Field B					
May	7.49	4.861	1.03	0.162	0.93
Jun	5.46	2.312	0.98	0.088	0.98
Jul	4.31	1.736	0.95	0.056	0.99
Aug	4.88	4.801	1.47	0.214	0.94
Sep	3.45	3.780	1.01	0.110	0.97

[z]* denotes a value significantly greater than zero as determined by Student's t-test with $n - 2 = 2$ df; t (0.975; 2) = 4.303 with $\alpha = 0.05$ and $n = 4$ (i.e., four pairs of plots per field).

The basic units of contagion or colony-forming units of *M. phaseolina* had a random spatial pattern. The random pattern of units of contagion for *M. phaseolina* was also confirmed from the values of Morisita's index and the appropriateness of only the Poisson distribution in 38 of 80 cases. This finding differs from that of Mihail and Alcorn (15) and that of our previous work (2,18) in which propagules of *M. phaseolina* were found to have a nonrandom or aggregated spatial pattern. The reason for this difference in findings probably lies in the spatial scale or size of experimental unit in which the studies were conducted. In the present study, we examined spatial pattern at a much smaller scale than in previous studies. Our total area for each plot of 25 quadrats was no larger than 90 × 90 cm, whereas the quadrats in other studies have been 1 × 0.3 m (15), 1 × 1 m (18), and 6 × 6 m (2). As an interpretation from the combined studies, it appears that the conclusion concerning the presence or degree of aggregation for *M. phaseolina* depends on the quadrat size used. With small quadrats, the pattern is random, but with larger quadrats, it is aggregated. The rationale for this phenomenon was suggested by Elliott (7, p. 69) and emphasizes the importance of choice of sample unit in spatio-temporal studies or propagules of soilborne plant pathogens, because changes in quadrat size can lead to differences in interpretation of the degree of randomness or aggregation of individuals in a population.

In addition to the potentially variable interpretation of spatial pattern, many nonbiological considerations also enter into the choice of a sampling unit for studies on soilborne pathogens. Some of these include the availability of variance estimates among and within sampling units and the resources available to conduct the study. In other cases, sampling units may be chosen to account for environmental variation. The amount of variation in propagule density of *M. phaseolina* within 18- × 18- or 15- × 15-cm quadrats was somewhat greater than we expected and may suggest another, as yet unidentified, spatial scale of interest for this fungus. Mean coefficient of variation values of between 20 and 40% with one sample/quadrat were probably not unacceptable. Additionally, the limited sample area and relatively high value for the ratio of cost per assay to cost per sample selected (3), necessitated the selection of one sample/quadrat per time.

Because the pattern of propagules was random within the 90- × 90-cm or 75- × 75-cm plots at both sites in this study, this may suggest these dimensions as a reasonable quadrat size for future studies. With the random pattern at this spatial scale, a few samples or one bulk sample from several soil cores within a quadrat should be sufficient to estimate propagule density with a minimum degree of variation. Also, since propagule density and spatial pattern did not vary significantly during the 5-mo period of the growing season, sampling for *M. phaseolina* can probably be conducted at any convenient time during the May-September period in temperate zone regions.

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