Quantification of *Pythium ultimum* var. *sporangiiferum* Zoospore Encystment Patterns Using Geostatistics

L. M. Dandurand, G. R. Knudsen, and D. J. Schotzko

Research Scientist, Associate Professor, and Research Associate, respectively, Department of Plant, Soil and Entomological Sciences, University of Idaho, Moscow 83844-2339.

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ABSTRACT

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Geostatistical analysis was used to quantify spatial patterns of encysted *Pythium ultimum* var. *sporangiiferum* zoospores on pea roots. In one experiment, peas were grown in sand at 20 C for 5 days, then roots were exposed to zoospore suspensions of *P. u. sporangiiferum* (150, 1,500, or 15,000 zoospores/g sand). After 3 h, roots were removed from the sand, stained with 0.05% trypan blue, and zoospore counts were made at 100×, using each square (83 × 83 μm) of a 10 × 10 reticle as a sample unit. Coordinates and number of encysted zoospores were recorded for each sample unit. Spatial statistics (geostatistics) were used to create covariograms and fit a spherical model for each inoculum density level. Fitted models provided estimates of the size of the spatial influence (range) in each treatment, random (nonspatial variation), or measurement error (nugget), and the value (sill) around which the variogram became stable. The spatial organization of cysts changed with inoculum density. At low and intermediate densities cysts were either randomly or uniformly distributed over the root surface. At the highest inoculum density, cysts had an aggregated spatial arrangement (nugget ≈ 0.41, sill ≈ 1.0, range ≈ 355 μm). When peas were exposed to zoospores after 2, 3, or 5 days after planting, spatial patterns of encysted zoospores again showed spatial structure only at the high inoculum density. Root system age did not affect spatial patterns.

Most natural environments are spatially structured by various energy inputs that result in patchy structures or gradients (23). Thus, biological organisms are rarely distributed in a random or uniform manner. The rhizoplane is a good example of this, since energy input is largely due to root exudates, and certain zones of roots produce more exudates than others. Spatial variability of exudates from seeds and roots may influence sites of colonization by rhizoplane microbes. Sites may be preferentially colonized by some rhizoplane microbes, and thus be no longer available to others (6–8). For example, chemotaxis of zoospores of pythiaceous fungi toward roots is regulated by root exudates (5,8,13,26,31,39), and higher accumulations of encysted zoospores have been reported to occur in the zone of root cell elongation, where a major portion of diffusible compounds are exuded (5,13, 26,30,31). Although the tendency for rhizosphere microbial populations to conform to lognormal or similar frequency distributions has been noted (1,24,27), there has been less attention paid to mechanisms of how population development leads to such distributions. Although the published literature contains information on microbial colonization of roots, and observations that rhizosphere microbes appear to be in aggregates, there is a need for appropriate quantitative spatial analysis describing how associations of rhizosphere microbes evolve over time. *Pythium ultimum* represents a logical choice as a model organism to investigate spatial-temporal interactions because certain sites on the host appear to be important for pathogen entry. The use of zoospores allows easy quantification of available inoculum, accurate timing of the pathogen's initial attack on roots, uniform access by the pathogen to the infection courts, and relatively easy quantification of attack sites.

Spatial statistical analysis provides a mechanism to explore processes that generate different patterns of organisms over time, and to determine the sensitivity of pattern to variations in these processes. Spatial variation is not a static property of natural populations, but changes with the number of individuals in a population or with changes in the sites that are available for occupation. Spatial analysis is defined here as quantitative evaluation of variations or changes in spatial orientation of an entity or population within a defined area or volume. Such an analysis requires that the spatial integrity (spatial coordinate framework) of the observations be maintained. Geostatistics is a method of spatial analysis that determines the degree of association (correlation) among samples based on the direction and distance between them (17,37,38). Although geostatistics evolved primarily through mining applications (20), it has proven highly applicable to biological systems; for example, geostatistics has been effectively used to evaluate insect spatial distributions (21,33–35) and a spatial simulation model (22), as well as plant disease patterns (3,18,28).

In geostatisitical analysis, covariograms, plots of the covariance of sample pairs against the distance (lag) between sampling points, are used to reveal the degree of association and dependence of spatially related data (spatial structure). Standardized covariograms allow comparison of changes in spatial structure that are independent of the overall population variance. Three key aspects of a covariogram are *(1)* the *sill, (2)* localized discontinuity (*"nugget"* or *y*-intercept), and *(3)* the *range.* The sill of a covariogram is the point at which the covariance no longer increases, where sample pairs become spatially independent. Localized discontinuity or nugget is a measure of nonspatial variation and measurement error. The structure or randomness (nonspatially structured variation) of the variation below the experimental scale cannot be determined or inferred without sampling at a smaller or larger scale (scale dependence). However, the proportion of the total variation that is below the sampling scale is estimated by the localized discontinuity. The range (range of spatial dependence) is the distance to the sill (*h*). Modeling of a covario-

gram is concerned with the response between the localized discontinuity and the sill, and reveals the spatial structure. Spatial dependence is the degree of association of any two points at a given separation distance revealed by the spatial structure. Thus, geostatistics detects spatial dependence among neighboring samples and defines the degree of dependence by giving quantifiable parameters.

The objectives of this study were to evaluate spatially the distributions of encysted zoospores of the plant pathogenic fungus *Pythium ultimum* Trow var. *sporangiiferum* Drechs. on the roots of pea seedlings, in response to changes in zoospore density and age of the roots.

MATERIALS AND METHODS

Organisms used. For all experiments, pea (*Pisum sativum* L. 'Columbia') seeds were used. *Pythium u. sporangiiferum* ATCC 13647 was maintained on cornmeal agar slants at 4 C. Zoospores were produced by growing mycelial mats for 2 days in V8 juice broth that were then rinsed twice with sterile distilled water and resuspended in mineral salts solution (25) for an additional 2 days. Zoospore release was induced by incubating the mycelial mats for 30 min at 4 C. Zoospore densities were quantified using a hemacytometer and adjusted, as appropriate, by dilution with mineral salts solution.

Plant growth conditions. Pea seeds were surface sterilized in 5% sodium hypochlorite for 5 min, followed by several rinses in sterile distilled water. Commercially obtained silica sand (Lane Mountain 20/30 mesh size; Lane Mountain Silica Co., Valley, WA) was sterilized by autoclaving, and added (100 g per tube) to opaque plastic seedling tubes (4 × 20.5 cm, Steuwe & Sons, Inc., Corvallis, OR). Peas (one pea per tube) were then placed on the sand surface and were covered with an additional 35 g of sand. Matric potential of the sand was adjusted and maintained at approximately −30 kPa over the course of each experiment, using distilled water. Seedling tubes were placed in racks in a growth chamber at 20 C, with a photoperiod of 16 h of light (fluorescent and incandescent) and 8 h of dark.

Effect of zoospore density on encystment patterns. Peas were planted as described, and after 5 days zoospore suspensions of *P. u. sporangiiferum* were added to each seedling by gently pouring them into the tubes. Zoospores were added at densities of 150, 1,500, or 15,000 zoospores/g of sand. After a 3-h incubation, plants were removed, gently washed with water, and root systems were excised at the point of emergence from the seed. After 5 days growth, no lateral roots had emerged and average root length was 2.0 cm. Entire roots were stained with 0.05% trypan blue in lactic acid/glycerine (1:1 v/v), and observed microscopically (100×). Numbers of encysted zoospores were counted over the entire visible root surface (one 83-μm wide row along each lateral root edge was omitted from the counts), using each square of a 10 × 10 reticle (83 μm × 83 μm) as a sample unit. Spatial coordinates (x, y) and number of zoospores were recorded for each sample unit. There were three replicates per treatment, and the experiment was repeated.

Effect of root age on zoospore encystment numbers and patterns. Peas were planted as described above. After 2, 3, or 5 days, zoospore suspensions were added at densities of 500, 2,000, or 8,000 zoospores/g. After a 3-h incubation, plants were removed, washed, stained, and observed as above. Average root lengths from 2-, 3-, or 5-day-old seedlings were 0.5, 1.0, and 2.0 cm, respectively. There were three replicates per treatment, and the experiment was repeated.

Statistical analysis. For each experiment, regression analysis was used to compare numbers of encysted zoospores per unit root area for the different treatments, using the SAS procedure GLM (32).

Geostatistical analysis of zoospore encystment patterns was done using covariance. Sample covariance C^D of a defined spatial integral (D) was graphed as a function of the separation distance (h) between points. The calculation of $C^D(h)$ at each separation distance in a data set was:

$$C_D(h) = 1 / n(h) \sum_{i=1}^{n(h)} z(x_i) \cdot z(x_i + h) - m_D(h) \cdot m_D(-h)$$

where $z(x^i)$ is the measured sample value at point x_i, $z(x_i + h)$ is the value at point $x_i + h$, $m_D(h)$ is the mean of all values that appear as $z(x_i + h)$, $m_D(-h)$ is the mean of all values that appear as $z(x_i)$, and $n(h)$ is the total number of sample pairs for any separation distance. The resulting plot of $C_D(h)$ versus the distance separating points is referred to as the covariogram (17). The shape

TABLE 1. Numbers of *Pythium ultimum* var. *sporangiiferum* zoospores encysted on 5-day-old pea roots at various inoculum densities

Experiment 1		Experiment 2	
Density (zoospores/g)	Zoospores/ 0.007 mm²	Density (zoospores/g)	Zoospores/ 0.007 mm²
150	0.02[z]	500	0.13[z]
1,500	0.40	2,000	0.36
15,000	1.25	8,000	1.19

[z] Regression analyses indicated inoculum density significantly affected numbers of zoospores encysted per unit area of root, $P \leq 0.05$.

TABLE 2. Spatial statistics from geostatistical analysis of *Pythium ultimum* var. *sporangiiferum* encysted zoospores at three different densities including: nugget, sill, range of spatial dependence, model R^2, covariance at the first lag (FL), lowest covariance value (LCV), and lag position at the lowest covariance value (LP)

Direction	Density[x]	Nugget	Sill	Range (μm)	R^2	FL	LCV	LP
Omni	150	ND[y]	ND	ND	ND	0.97 a[z]	0.97	1
	1,500	ND	ND	ND	ND	0.84 b	0.84	1
	15,000	0.56	0.97	332	0.92	0.69 c	0.69	1
45°	150	ND	ND	ND	ND	0.99 a	0.99	1
	1,500	0.76	1.00	140	0.68	0.93 a	0.93	1
	15,000	0.63	0.96	468	0.97	0.76 b	0.76	1
90°	150	ND	ND	ND	ND	0.98 a	0.98	1
	1,500	0.51	0.99	231	0.97	0.80 b	0.80	1
	15,000	0.47	0.97	334	0.98	0.69 b	0.69	1
135°	150	ND	ND	ND	ND	0.98 a	0.97	1
	1,500	0.70	0.98	239	0.79	0.89 a	0.89	1
	15,000	0.53	0.96	404	0.86	0.77 b	0.77	1
0°	150	ND	ND	ND	ND	0.91 a	0.91	1
	1,500	0.30	0.99	226	0.81	0.79 a	0.79	1
	15,000	0.41	0.97	355	0.90	0.59 b	0.59	1

[x] Five-day-old peas were inoculated with 150, 1,500, or 15,000 zoospores/g sand.

[y] Not determined.

[z] Mean covariance values at first lag position for each direction followed by same letter are not significantly different ($P > 0.05$) according to orthogonal contrast analysis.

of this plot defines the type of spatial structure and range of spatial dependence. Covariances were calculated with a C language program (Agricultural Software Development Group, University of Idaho, Moscow). The presence or absence of anisotropic patterns was determined by examination of the covariograms for the 0°, 45°, 90°, and 135° axes, where 0° represents the direction along the length of the root. A spherical model was fit to each data set using the least squares approach of Cressie (4). Fitted models provided estimates of the size of the spatial influence (range) in each treatment, random or measurement error (nugget), and the value (sill) around which the covariogram became stable. For our purposes, computed $C_D(h)$ values were divided by the

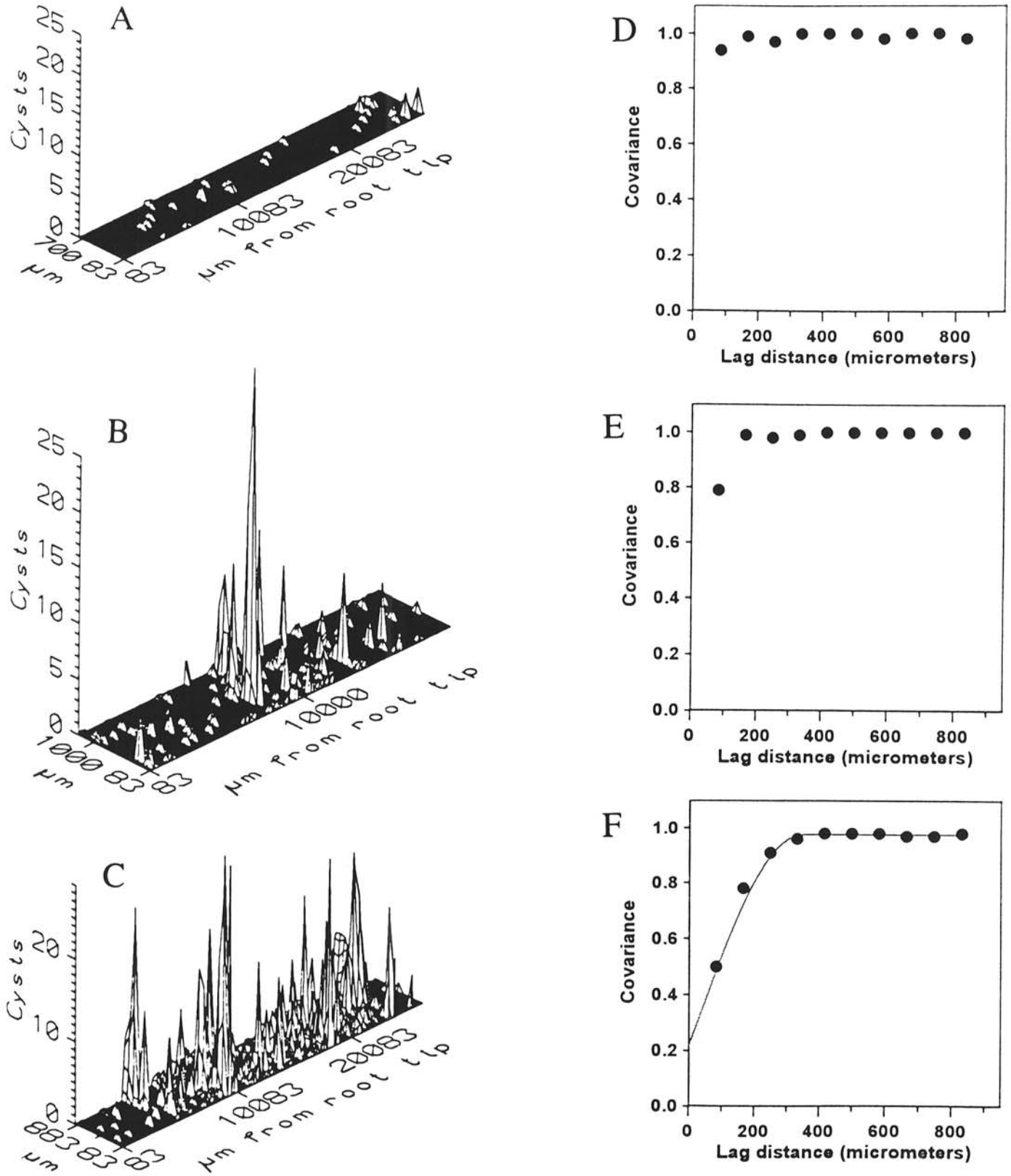

Fig. 1. Maps of spatial pattern of *Pythium ultimum* var. *sporangiiferum* zoospores for representative pea root samples inoculated at **A,** 150, **B,** 1,500 or **C,** 15,000 zoospores/g. Corresponding covariograms for each map at inoculum densities of **D,** 150, **E,** 1,500, or **F,** 15,000 zoospores/g at an angle of 0° direction (along length of the root).

sample covariance to provide a common scale for comparing standardized covariograms. This treatment of spatial estimators is a common geostatistical procedure when comparisons of spatial statistics between different sampling units or locations are important (17). This creates a sill that should be close to 1, irrespective of the sample variation.

RESULTS

Effect of zoospore density on encystment numbers and patterns. Average numbers of zoospores encysted on pea roots in both experiments differed significantly for the various inoculum densities tested (Table 1).

Results of spatial analysis of zoospore encystment patterns for inoculum densities of 150, 1,500, or 15,000 zoospores/g are shown in Table 2. Treatment by experiment interactions was not significant ($P > 0.05$), and data from both repetitions were pooled. The parameters shown include covariance at the first lag distance (i.e., one sample unit, or 83 μm, away), the lowest observed covariance value, the lag position at which the covariance was lowest, the range of spatial dependence and sill when a spherical model was fit to the covariance values, and the model coefficient of determination (R^2). Representative spatial patterns of zoospore encystment along with corresponding covariograms are shown in Figs. 1A–F.

Geostatistical analysis detected nonrandom patterns of zoospore encystment on roots inoculated with 15,000 zoospores/g. As revealed by the shapes of covariograms, encysted zoospores were aggregated on the surface of pea roots (Fig. 1F). At this density, covariance values were fit to a spherical model that typifies an aggregated spatial structure, and that provides a measure of spatial dependence and structure. A greater degree of spatial dependence was evident in the 0° direction compared with 45°, 90°, or 135°, indicating anisotropy along the length of the root (Table 2). As estimated from the covariance at the first lag position, approximately 41% of the total variation was spatially structured along the length of the root (Table 2, Fig. 1F). In this direction, spatial dependence (range of influence) was 355 μm. When roots were inoculated with 150 zoospores/g, the spatial pattern of encysted zoospores was either random or uniform (Table 2). Covariograms were essentially flat (Fig. 1D), indicating that the amount of variability observed was not due to spatial orientation (Fig. 1E). Therefore, models were not fit to these covariances. When inoculum density was increased to 1,500 zoospores/g the average covariance value at the first lag position was 0.79 in the direction of greatest anisotropy (0°) indicating that only about 21% of the total variation was spatially structured along the length of the root (Table 2, Fig. 1E). However, spatial structure and dependence at this inoculum density were highly variable among replicates. Our interpretation of the variability observed at this inoculum density is that here, spatial structure and dependence of encysted zoospores are becoming evident. A significantly smaller proportion of the total variability was spatially dependent at 150 or 1,500 zoospores/g than at 15,000 zoospores/g (Table 2).

Effect of root age on zoospore encystment numbers and patterns. No temporal effect on patterns of zoospore encystment was observed for either repetition of the experiment. The shape of the covariograms and the magnitude of the covariance for a given density did not change significantly with root age. Also, the interaction between root age and inoculum density was not significant. Density effects in this experiment were similar to those described above. Little spatial structure was evident at a density of 500 zoospores/g (Table 3), while a significantly greater amount of the total variability was spatially structured when plants were inoculated with 8,000 zoospores/g. At this density, approximately 35% of the total variability was structured along the length of the root, and the range of spatial dependence was 312 μm. At 2,000 zoospores/g, approximately 22% of the variability was structured along the length of the root. However, the spatial dependence at this density was not significantly different from spatial dependence at either 500 or 8,000 zoospores/g (Table 3).

DISCUSSION

Distinctive spatial organization of encysted zoospores developed with changes in inoculum density. At low inoculum densities, cysts were either randomly or uniformly distributed over the root surface, whereas at high inoculum densities, nonrandom spatial patterns of encystment were evident. Encysted zoospores were highly aggregated on the rhizoplane of pea roots. When 2-, 3-, and 5-day old seedlings were exposed to *P. u. sporangiiferum* zoospores, spatial analysis indicated no influence of root age on spatial pattern of zoospore encystment.

Our findings confirm an earlier report that zoospores may encyst in a nonrandom or aggregated pattern (40). However, our findings further indicate that aggregation of encysted zoospores on the rhizoplane of pea roots is limited to high inoculum densities. In addition, we found that zoospores of *P. u. sporangiiferum* encysted throughout the root region in a nonspecific manner. This contrasts with other host-pathogen combinations such as *Pythium dissotocum* and cotton, in which zoospores encyst specifically on the root border cells (12), or *Pythium aphanidermatum,* which preferentially encysts in the zone of elongation of cucumber roots (40).

Statistical descriptions of spatial patterns do not by themselves provide an explanation of the mechanisms responsible for any

TABLE 3. Spatial statistics from geostatistical analysis of *Pythium ultimum* var. *sporangiiferum* encysted zoospores at three different densities including: nugget, sill, range of spatial dependence, model R^2, covariance at the first lag (FL), lowest covariance value (LCV), and lag position of the lowest covariance value (LP)[w]

Direction	Density[x]	Nugget	Sill	Range (μm)	R^2	FL	LCV	LP
Omni	500	ND[y]	ND	ND	ND	0.96 a[z]	0.96	1
	2,000	0.75	0.99	277	0.78	0.89 b	0.89	1
	8,000	0.60	0.99	317	0.97	0.80 c	0.80	1
45°	500	ND	ND	ND	ND	0.95 a	0.95	1
	2,000	ND	ND	ND	ND	0.90 a	0.90	1
	8,000	0.63	1.00	381	0.85	0.86 a	0.86	1
90°	500	ND	ND	ND	ND	0.98 a	0.96	2
	2,000	ND	ND	ND	ND	0.91 a	0.85	1
	8,000	0.46	0.99	202	0.85	0.79 b	0.79	1
135°	500	ND	ND	ND	ND	0.97 a	0.95	2
	2,000	ND	ND	ND	ND	0.97 a	0.95	2
	8,000	0.74	0.99	315	0.84	0.90 b	0.90	1
0°	500	ND	ND	ND	ND	0.94 a	0.94	1
	2,000	0.63	0.99	353	0.69	0.78 ab	0.78	1
	8,000	0.37	0.99	312	0.94	0.65 b	0.65	1

[w] Values shown are averages of 2-, 3-, and 5-day results.
[x] Two-, three-, or five-day-old peas were inoculated with 500, 2,000, or 8,000 zoospores/g sand.
[y] Not determined.
[z] Covariance values at first lag position for each direction followed by same letter are not significantly different ($P > 0.05$) according to orthogonal contrast analysis.

pattern (2,11,15). However, characterizing spatial variability may provide insight into what is causing it (29). For encystment of *P. u. sporangiiferum* zoospores on pea roots, the spatial patterns observed were density dependent. Roots and their exudates have been shown to be chemoattractants for zoospores of pythiaceous fungi (10,13,14,31,39). However, sites of attraction and encystment vary with the host-pathogen combination. For example, Goldberg et al (12) found that *P. dissotocum* was specifically attracted to cotton root border cells, but nonspecifically attracted to roots of *Agrostis palustris, Lactuca sativa* and *Salicornia. Pythium catenulatum* was not preferentially attracted to cotton root border cells but encysted along the entire root surface of *Cucumis sativus, A. palustris, L. sativa,* and *Salicornia* (12). Thus, chemotaxis to specific sites of exudation on roots may not be the only explanation for observed aggregates at high densities. Thomas and Peterson (36) suggested that zoospore aggregation may be a dual-component chemotactic process that is triggered by exogenous attractants and amplified by chemical signals from aggregating spores. Jones et al (19) proposed that while chemoattractants are at least partly responsible for encystment on roots, surface-mediated events are probably also involved. We propose two possible explanations for our observations of spatial patterns of encysted zoospores on pea roots. The first is that chemoattractants from roots act as general signals for zoospores that, initially, encyst randomly on roots. As the density of encysting zoospores reaches a certain threshold, chemoattractant signals released from them reach an effective concentration, which then results in the formation of aggregates. As suggested by Deacon and Donaldson (9) attraction of zoospores to aggregates may be a response to Ca^{2+}, which is known to be released during encystment (16). If autoaggregation were not a factor in encystment, one would expect uniform or random spatial patterns of encysted zoospores even at high densities. The alternative explanation is that the underlying source of chemoattractant from the root is spatially patterned, in which case aggregation may be the result of intraspecific competition for specific sites on the root.

In these experiments, spatial statistical analysis provided a quantitative evaluation of spatial variability in patterns of *Pythium* zoospore encystment, as well as insight into zoospore behavior. Observational data on patterns of interacting microbes may also provide insight into how microbes partition resources and coexist on the rhizoplane.

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