Spatial Pattern Analysis of Disease Severity Data for Alfalfa Leaf Spot Caused Primarily by *Leptosphaerulina briosiana*

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This research was supported in part by a grant from the National Crop Loss Design Committee, U.S. Department of Agriculture/Cooperative State Research Service.

Journal Series Paper 9783 of the North Carolina Agricultural Research Service, Raleigh 27695-7601.

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The authors wish to thank Larry Nelson and Robert I. Bruck for helpful comments provided and Charles R. Harper and Cynthia K. Ragland for assistance in this study.

Accepted for publication 10 September 1985 (submitted for electronic processing).

ABSTRACT

Thal, W. M., and Campbell, C. L. 1986. Spatial pattern analysis of disease severity data for alfalfa leaf spot caused primarily by *Leptosphaerulina briosiana*. Phytopathology 76:190-194.

Disease severity data from grids of contiguous quadrats were used to investigate spatial pattern of alfalfa leaf spot, which is caused primarily by *Leptosphaerulina briosiana*. Three methods of analysis were used: discrete probability distributions, indices of dispersion, and a blocked quadrat variance method. A range from regular to moderately aggregated disease pattern was found among the samples. Distributional techniques generally did not allow differentiation of spatial pattern among samples. Indices of dispersion generally indicated a regular to random pattern in the data at the quadrat level, although slight clustering was indicated in a few cases. Taylor's *b* was estimated on both a field and plant-to-plant (within quadrat) basis and indicated a greater degree of aggregation at the plant-to-plant level than at the field level. The blocked quadrat variance method showed multiple peaks in the mean square versus block size plots which may indicate clustering at several scales.

Botanical epidemiologists have directed a large portion of their efforts to the study of disease progression over time, but have, until recently, generally neglected the spatial aspects of disease (7). Knowledge of disease pattern in space is important because the pattern can affect progression of disease and the consequences of the disease (1,2,18).

Spatial pattern analysis is useful in providing a quantitative characterization of disease within a field; for providing insight on the dynamics of the host, pathogen, and environmental interaction within a pathosystem; and for providing a basis for the development of sampling procedures (e.g., determination of sample size, proper size of sampling units, and the need for stratification) (2). Spatial pattern in biological systems has been studied extensively by ecologists (11,19) and to a limited extent by plant pathologists (3,7,16). Pattern is generally described as ranging from regular to random to aggregated, and attempts have been made to quantify the position of a population within this continuum.

Numerous analytical tools, including discrete probability distributions, indices of dispersion, and blocked quadrat variance methods have been used by ecologists in studying spatial pattern. The application of frequency distributions to biological data has been discussed widely (5,11,17,19,21) and, in many instances, a particular distribution can arise from several alternative sets of hypotheses. Thus, distribution fitting cannot be used to determine underlying biological processes (9,17), but may be useful as a preliminary indication of the degree of aggregation found at the quadrat size under consideration in an ecosystem.

Indices have been developed to measure the degree of aggregation in a population. Elliott (5) summarizes many of these, and gives expected values of these indices for regular, random, and aggregated populations. One common index is the variance-to-mean ratio ($s^2/\bar{x}$) which has the value 0 at maximum regularity, 1 when a random pattern is present, and Σx when maximum aggregation is present in the system. The value of $s^2/\bar{x}$ is highly dependent on mean density ($\bar{x}$) for aggregated populations (19) but is useful for indicating randomness. Values of Morisita's index (I_δ) range from $1-[(n-1)/((\Sigma x)-1)]$ at maximum regularity, to 1 for randomness, and n for maximum aggregation when n is the number of sampling units. The index is not greatly affected by the mean density ($\bar{x}$) or Σx, but is a strong function of n for populations with nonrandom spatial patterns.

Taylor (22) described a function [$s^2 = ax^{-b}$] which relates the variance of a population (s^2) to a power of its mean ($\bar{x}$). The parameter a is a scaling factor which depends chiefly on the size of the sampling unit, and b is an index of dispersion which varies from 0 for regular, to 1 for random, and approaches infinity for highly aggregated populations. He gives examples of b values ranging from 0.7 to 3.08 for sample populations of numerous species.

Blocked quadrat variance methods (10), are based on changes in mean squares for successive groupings of contiguous quadrats. Groupings of 1, 2, 4, 8, ..., $N/2$ contiguous quadrats are used, in which N is the number of quadrats in a grid. The method is best suited to grids containing a power of 2 as the number of quadrats (e.g., 256) so that all quadrats are used at each level of grouping. Other methods, such as Hill's (14) use the data more efficiently than Greig-Smith's (10), but are more suited to transect data. In the blocked quadrat variance method, peaks in the plot of mean square versus block size occur when blocks align with clusters of disease since this causes large differences in block means; thus peaks are used to indicate scales of aggregation.

The objective of the present study was to characterize the spatial pattern of leaf spots within production type alfalfa fields and to seek plausible biological, cultural, or environmental hypotheses to account for the observed spatial patterns.

MATERIALS AND METHODS

Description of samples. A total of five alfalfa fields in Wake, Rowan, and Forsyth counties in NC were sampled for leaf-spot

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severity during the spring and summer of 1982 (Table 1). Samples were collected on a 16 × 16 grid of 1 m square quadrats (256 quadrats total) between 22 March 1982 and 28 May 1982; grid size was decreased to an 8 × 8 grid (64 quadrats total) for samples taken from 3 June 1982 to 27 August 1982 due to time considerations. In Wake County, a grid of quadrats was established in field 1A and the same location was sampled nine times during the growing season. In a second grid in the same field (identified as Wake 1B) three samples were obtained between March and June. For all other locations, fields, or sites within fields, a grid of quadrats was sampled only once.

Quadrats were marked by setting up a grid of flags at two meter intervals with each 2 × 2 meter quadrat divided visually into four 1 meter square quadrats. Stem density was determined by countin the number of stems in one arbitrarily chosen area 30 × 30 cn within each quadrat of the grid. Three stems were selected arbitrarily from each quadrat and taken to the laboratory in coolers. A severity rating was obtained for each stem by visually estimating percent diseased leaf area on a randomly chosen sample of two lower and two upper leaves from each stem (*unpublished*). Each leaf sampled was compared to a visual assessment key. The key followed a scale similar to the Horsfall-Barratt rating system (12) and was based on the keys of James (13).

Leaf-spotting pathogens. Several fungi are known to cause leaf-spots on alfalfa (8). Leaf spots can sometimes be differentiated on the basis of characteristic symptoms, but this should be confirmed by isolations. In the present samples, isolations indicated that *Leptosphaerulina briosiana* (Poll.) Graham & Luttrell was the predominant leaf-spotting pathogen (*unpublished*).

Distribution fitting. The positive binomial, Poisson, Poisson with zeros, and negative binomial probability distributions were fitted to quadrat disease severity values by using a FORTRAN program (6). A class size of 1% was used in grouping the data for fitting the distributions. In samples where the number of classes was large, a class size of 2% was also used. When the class variance was less than the mean, only the positive binomial, Poisson, and Poisson with zeros distributions were fitted. A nonsignificant value for the Chi-square statistic indicates the data do not differ significantly from the distribution, and is thus interpreted to mean that the distribution adequately described the sample data.

Indices of dispersion. The variance-to-mean ratio was calculated as:

$$s^2/\bar{x} = [\Sigma(x-\bar{x})^2]/[(n-1)\bar{x}] \quad (1)$$

and Morisita's index (16) was calculated as

$$I_\delta = n\left\{[\Sigma x(x-1)]/[\bar{x}(\Sigma x - 1)]\right\}$$
$$= n\left\{[\Sigma(x^2)-\Sigma x]/[(\Sigma x)^2-\Sigma x]\right\} \quad (2)$$

in which x is the estimated percent diseased leaf area of an individual quadrat, $\bar{x}$ is the arithmetic mean of all quadrats on a grid, and n is the number of sampling units. The form of Taylor's function is:

$$s^2 = a\,\bar{x}^{\,b}. \quad (3)$$

TABLE 1. Location, date, cultivar, plant density, mean disease severity, values of indices of dispersion, and peaks in plots of mean square versus block size for 19 samples obtained to examine the spatial relationships of alfalfa leaf spot caused primarily by *Leptosphaerulina briosiana*

County and field[v]	Date[w]	Alfalfa cultivar	Plant density (no./m²)	Disease severity (%)	$s^2/\bar{x}$[x]	I_δ[x]	Taylor's b[y]	Peaks in plot of mean square versus block size[z]														
								x-direction								*y*-direction						
								1	2	4	8	16	32	64	128	1	2	4	8	16	32	128
Wake																						
1A	22 Mar	Arc	–	2.2	0.6	0.8	1.6				★	★				★			★		★	★
	2 Apr		–	2.4	0.4	0.7	2.7			★		★							★			★
	22 Apr		319	2.9	0.7	0.9	2.5	★				★		★			★				★	
	28 May		586	5.3	0.7	1.0	2.6			★		★				★			★			
	28 Jun		333	7.5	1.5	1.1	2.6				★		★			★			★			
	15 Jul		300	4.5	1.0	1.0	2.6	★		★			★			★			★			
	2 Aug		274	2.4	0.5	0.9	2.5	★					★				★			★		
	10 Aug		214	2.8	0.8	0.9	1.8			★			★			★				★		
	27 Aug		175	6.4	0.7	1.0	2.5		★			★				★		★			★	
1B	26 Mar	Arc	–	2.1	0.3	0.7	1.7	★		★					★		★		★			★
	15 Apr		308	2.8	0.6	0.9	2.6			★		★								★		★
	3 Jun		536	9.3	1.4	1.0	2.3		★		★		★			★		★		★		
2A	17 Aug	Arc	456	6.6	0.9	1.0	2.9		★		★										★	
Rowan																						
1A	16 Apr	Cimmaron	1,214	2.2	0.4	0.7	2.0		★				★		★	★				★		★
1B	25 May		1,164	6.3	1.4	1.1	2.3	★				★			★	★		★			★	
2A	16 Apr	Cimmaron	567	2.9	1.1	1.0	1.6				★		★		★	★				★		
2B	25 May		689	11.9	1.6	1.1	2.4	★			★					★		★			★	
Forsyth																						
1A	22 Jul	Classic	281	4.9	0.9	1.0	2.1			★			★					★			★		
1B	22 Jul		453	5.5	0.6	0.9	2.0	★		★			★				★		★			

[v] Numbers refer to fields, letters refer to grids of quadrats at arbitrarily selected locations within a field.

[w] Prior to June, all samples were from 16 × 16 grids of quadrats; during June, July, and August, all samples were from 8 × 8 grids.

[x] A value of 1.0 for the variance-to-mean ratio ($s^2/\bar{x}$) or Morisita's index (I_δ) indicates randomness, a value less than 1.0 indicates regularity, and a value greater than 1.0 indicates aggregation.

[y] Taylor's b was calculated by regression analysis from the equation $\log s^2 = \log a + b \log \bar{x}$; the interpretation of values is the same as for the variance-to-mean ratio or Morisita's index.

[z] Analyses were done in two directions since block sizes of 2, 8, 32, and 128 are asymmetrical; the y direction corresponds to the orientation of the long axis of the asymmetrical blocks and with the direction which would be followed by harvest machinery.

The parameters a and b were estimated by using a log transformation of equation 3:

$$\log s^2 = \log a + b \log \bar{x} \quad (4)$$

and using linear regression to estimate $\log a$ and b. Taylor's b was estimated on two scales: for each of the 19 samples, the values of mean disease for each individual quadrat were regressed on the variances of the three stems within those quadrats; and an overall b was estimated based on all 19 samples by regressing the mean percent disease leaf area value of each sample on the variance of the quadrats for that sample.

Blocked quadrat variance methods. The method of Greig-Smith (10) employs data from contiguous quadrats arranged either on a grid or a transect. Adjacent quadrats were successively grouped and a nested structure given to the data with blocks of 1, 2, 4, 8, 16, ..., $N/2$ quadrats, when N is the total number of quadrats in the grid (either 64 or 256 in this study). Blocks of 2, 8, 32, 128 ... quadrats are asymmetrical. Mean square estimates for successive block sizes were obtained from a nested ANOVA in both an x-axis and y-axis direction since the orientation of a plot of quadrats may influence the results of the analysis (10). The y-axis direction was oriented to correspond to the direction harvesting machinery would follow in a field. Peaks in the plot of mean square versus block size were interpreted to indicate clumping or aggregation at that block size.

RESULTS

Goodness of fit of sample data to the five probability distributions is given in Table 2. The distribution fitting method generally did not adequately describe the data from the 16 × 16 grids. In four samples, the Poisson with zeros had a nonsignificant chi-square ($P = 0.05$) which indicated a lack of difference between the observed and predicted frequency distribution for these samples. In most of these samples, however, the Poisson and positive binomial distributions also gave acceptable fits. In three cases with 8 × 8 grids, the variance exceeded the class mean and all five distributions gave nonsignificant chi-square values. Means and variances presented in Table 2 were calculated based on class designations.

Estimates for the indices of dispersion and peak of the mean square versus block size plots are given in Table 1. The $s^2/\bar{x}$ for the overall sample ranged from 0.29 to 1.6, indicating a range from nearly regular occurrence to some aggregation of disease at the quadrat level. I_δ ranged from 0.66 to 1.06. Many of the values for I_δ were near 1.0, indicating a lack of aggregation of disease at the

TABLE 2. Goodness-of-fit of alfalfa leaf-spot severity data to five probability distributions

Sample[x]	Class size[y]	Class mean[z]	Class variance[z]	Probability distributions:[w] Positive binomial	Poisson	Poisson w/zeros	Negative binomial	Neyman type A
W1A322	1	1.7	1.4	**	**	*	–	–
W1B326	1	1.6	0.7	**	**	**	–	–
W1A402	1	1.9	1.0	**	**	*	–	–
W1B415	1	2.3	1.7	**	**	NS	–	–
R1A416	1	1.7	1.0	**	**	NS	–	–
R2A416	1	2.4	3.2	**	**	**	**	**
	2	0.9	0.9	*	*	NS	–	–
W1A422	1	2.4	2.1	**	**	NS	–	–
R1B525	1	5.8	9.0	**	**	**	**	**
	2	2.7	2.4	**	**	**	–	–
R2B525	1	11.4	19.5	**	**	**	**	**
	2	5.5	5.0	**	**	**	–	–
W1A528	1	4.8	3.9	**	**	**	–	–
	2	2.2	1.1	**	**	**	–	–
W1B603	1	8.8	12.3	NS	NS	NS	NS	NS
	2	4.1	3.2	NS	NS	NS	–	–
W1A628	1	7.0	11.2	NS	NS	NS	NS	NS
	2	3.2	2.8	NS	NS	NS	–	–
W1A715	1	4.0	4.8	NS	NS	NS	NS	NS
F1A722	1	4.4	4.3	NS	NS	NS	–	–
	2	1.9	1.2	*	*	NS	–	–
F1B722	1	5.1	3.0	**	**	NS	–	–
	2	2.3	0.8	**	**	**	–	–
W1A802	1	2.0	1.4	**	**	NS	–	–
W1A810	1	2.3	2.1	NS	NS	NS	–	–
W1A827	1	5.9	4.4	NS	NS	NS	–	–
	2	2.7	1.2	**	**	*	–	–
W2A827	1	6.1	6.0	NS	NS	NS	–	–
	2	2.8	1.5	*	**	*	–	–

[w] Designation for sample-first letter refers to county, first number refers to field, second letter refers to location in field, and second number is the date, e.g., W1A322 is a sample from Wake County, field 1, location A taken on 22 March 1982. F = Forsyth County and R = Rowan County. All samples were collected in 1982.

[x] Size of frequency classes used in grouping severity data.

[y] Class mean and variance based on class size designated.

[z] Symbols: ** = significant chi-square at $P = 0.01$, * = significant chi-square at $P = 0.05$, NS = chi-square not significant at $P = 0.05$, and – = distribution not fit because class variance was less than the mean.

quadrat level. I_δ was less dependent on the mean severity level than $s^2/\bar{x}$.

Estimates of Taylor's b, based on variance and mean values for quadrats within each sample, ranged from 1.6 to 2.7 with a mean of 2.2, indicating aggregation at the within-quadrat or plant-to-plant scale. The estimate of b at the field (sample) scale, based on overall sample variance and mean estimates of all 19 samples, was 1.7, indicating a lower degree of aggregation at the field scale than was found for quadrats within a sample.

Plots of mean square versus block size had multiple peaks in almost all cases which may indicate more than one level of aggregation at a level greater than the single quadrat. Among the 19 samples, peaks occurred more frequently at block sizes of 1, 4, 16, and 32 for the x-direction analysis than at block sizes of 2, 8, 64, or 128. For the y-direction analysis, peaks occurred most frequently at a block size of 1 and peaks were encountered at block sizes 4-128 with nearly equal frequency (5–7 times per block size). Among the nine samples taken in field 1A in Wake County, peaks were more frequent at block sizes of 1, 4, 16, and 32 for the x-direction analysis than for other block sizes and most frequent at a block size of 1 for the y-direction analysis. A distinct shift in peaks occurred for block size 16 to block size 32 when grid size was reduced from 16 × 16 to 8 × 8 for field 1A in Wake County.

DISCUSSION

The results from the analytical methods used in this study must be interpreted with the biology of the particular pathosystem in mind. Alfalfa is grown as a broadcast (not row cropped) perennial crop that is harvested from three to six times per growing season in stands maintained for 3–6 yr. An alfalfa stand is a genetically heterogeneous population of plants. The pathogen, *L. briosiana*, produces relatively large, multicelled spores (26–46 × 11–18 μm) that are forcibly discharged from infected leaves on the plant, from hay which has been cut but not yet baled, and from leaf debris which remains after the baling operation.

The dispersion indices indicate in general, some degree of regularity at the sample or grid-of-quadrats level in the data for most of the samples taken early in the season (March to mid-April). For later samples (late April to August), the two indices generally agree in meaning. Estimates for I_δ were mostly near 1.0 after the first few samples, indicating randomness of disease distribution at the quadrat level. Several values of 1.1 were obtained for I_δ that indicate a slight tendency toward aggregation of disease at the sample level. The variance-to-mean ratio was less than 1.0 for early and late samples but was generally greater than 1.0 for samples taken from mid-April to mid-July. These later values for the $s^2/\bar{x}$ ratio, which indicate some degree of aggregation, generally were obtained when percent diseased leaf area was the greatest.

The values of Taylor's b obtained for each sample were consistently greater than 1.0. Whereas the $s^2/\bar{x}$ ratio and I_δ indicated regularity, randomness, or aggregation at the level of the whole sample or grid of quadrats, the values obtained for the calculation of Taylor's b for each sample represents the aggregation present within quadrats. Thus, the interpretation based on I_δ, $s^2/\bar{x}$, and Taylor's b would be that, in general, alfalfa leaf spots occur randomly or with slight regularity or slight aggregation when a single quadrat is the measured unit. When individual stems within quadrats are considered, disease is aggregated.

The plots of mean square versus block size often produced several peaks. Fourteen of 19 samples gave peaks at the 1- or 2-quadrat block size in the y-axis direction. Since the y-axis analysis was done to align asymmetrical blocks in the same direction as harvest machinery movement, a possible explanation for this aggregation at the 1 × 1-m or 1 × 2-m scale may be derived from harvest practices. Forage mowers used in all fields sampled cut an area approximately 2 m wide on each pass through the field. Harvested alfalfa may be left to dry in place or may be raked into strips 80-100 cm wide immediately for drying or just prior to baling operations. The alfalfa often dries in 1 or 2 days in the field prior to baling which would allow for the concentration of new inoculum from harvested material in an area approximately 1 m wide. Also, baling operations (for rectangular bales) would provide for increased leaf deposition in the approximately 1 m wide strip in the field. In each case, quadrats along the 1 m wide strip would tend to have more similar disease characteristics which may account for the 1 × 1-m or 1 × 2-m scale of aggregation frequently observed in the y axis direction in this study. Specific "ridges" of high and low disease levels would probably not occur because the baling strips would not necessarily occur in the same location at each harvest.

A shift in peaks occurred from a block size of 16 (4 × 4) in the 16 × 16 grid of quadrats to a block size of 32 (4 × 8) in the 8 × 8 grid for quadrats in field 1A in Wake County. This peak shift may be due to the particular quadrant of the 16 × 16 lattice which was selected for continued sampling on the 8 × 8 lattice. Since the peak at block size 32 was for the 8 × 8 grid of quadrats, this suggests that aggregation occurred at a size equivalent to one half of the 8 × 8 grid of quadrats.

The methods used in this study measure degree of aggregation at different scales. Taylor's b estimates based on quadrat means and variance within a quadrat provided an indication of aggregation at the plant-to-plant level. The other dispersion indices and the distributional methods indicate patterns at the quadrat level and the blocked quadrat variance method detected patterns at levels larger than a single quadrat. Aggregation of the disease was indicated at the plant level, whereas randomness or slight aggregation was indicated at the quadrat level. Aggregation also was indicated for certain larger block sizes, especially at block size 4 and in the 16 to 32 block size range.

The aggregation at the plant-to-plant is not unexpected since alfalfa is a genetically hetergeneous crop and plants within a cultivar may vary in level of resistance. Also, although the ascospores of *L. briosiana* are forcibly discharged, the spores are relatively large and are covered with a mucilaginous matrix for adhesion to surfaces. These spore characteristics may contribute to a greater degree of autoinfection than alloinfection, and thus contribute to aggregation at the plant level. The lack of aggregation at the quadrat level may be due to the averaging effect of the plant-to-plant aggregation and the spread of inoculum over time in a perennial crop. At the larger scales the aggregation may be due to a number of factors. Environmental patchiness due to differences in soil moisture, plant density, and elevation may occur at this level. Cultural practices such as harvest operations probably also contribute to patchiness at this larger scale.

The degree of aggregation appeared to increase as leaf spot severity increased in a field; however, this should be investigated for a larger range of disease severity values. It would also be helpful to investigate variation occurring at scales larger than the grid sizes used here. Additionally, the proportion of resistant plants and degree of resistance should be determined within a number of alfalfa cultivars and the aggregation or randomness of leafspot disease in those cultivars examined to ascertain the effect of host resistance in a mixed population of hosts on spatial aggregation of disease.

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