Special Topics

Two-Dimensional Distance Class Model for Quantitative Description of Virus-Infected Plant Distribution Lattices

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ABSTRACT

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The spatial pattern of virus-infected plants arranged on a variable sized lattice is analyzed by a two-dimensional, distance-class method. The method quantitatively estimates randomness of infected plants and is tolerant of missing data. Average size of the clusters of infected plants and their relative locations on the lattice (X, Y) coordinate) are presented. By using one infected plant as the origin, the distance between it and every other infected plant on the lattice is defined in horizontal (X) and vertical (Y) units. Pairs of infected plants are then categorized into two-dimensional, [X, Y], distance classes. The number of pairs of infected plants

in each distance class is counted and divided by the total number of pairs in that distance class. The process is repeated using each infected plant on the lattice as the origin. Computer simulations generate expected standardized count frequencies under the assumption of random pattern on the lattice. Levels of significance for the difference between observed and expected values are generated directly during the simulations. Theoretical and empirical sampling are used to demonstrate the power of the test to describe quantitatively the spatial pattern and to compare the two-dimensional analysis with ordinary runs and doublet analysis.

The spatial pattern of virus-infected plants within a field is a fundamental characteristic of the spread of the disease and of the initial inoculum or source of the disease. A random pattern is suggestive of primary spread from a source outside of the field. Conversely, clustering of infected plants may indicate secondary spread from a source within the field (11). Secondary spread of an insect-vectored virus need not result in an aggregation of adjacent plants, but may result in more loosely defined clusters of infected plants. Vector movement is usually not restricted to adjacent plants within rows, but can occur between proximate plants in all directions on the plane of the field (i.e. across rows, along rows or any degree of diagonal movement) (8). Analytical description of the spatial pattern of diseased plants is essential in evaluating disease spread; however, it is a difficult phenomenon to quantitate.

Freeman (5) introduced a method of doublet analysis which evaluates disease spread in all directions and is applicable where there are vacancies in the data; however, the analysis is limited to spread of the disease to directly adjacent or diagonally adjacent plants.

Madden et al (11) evaluated the ordinary runs test (6) and two versions of doublet analysis (4,15); ordinary runs were the best

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method for determining randomness of virus-infected plants. The three methods only considered the spread of disease between adjacent plants in one direction (within rows) and these methods were intolerant of missing data.

Proctor (14) described the spatial pattern of infected plants within a four by five lattice by grouping pairs of infected plants into distance-orientation classes. He defined a distance-orientation class as the number of horizontal (X) and vertical (Y) unit moves that separate a pair of infected plants from each other. The horizontal distance being the abscissa and the vertical distance is the ordinate. The point at which the abscissa and ordinate converge form the 90° angle of a right triangle. The distance between the pair of infected plants is the length of the hypotenuse and the orientation is the angular value between the abscissa and hypotenuse. The number of distance-orientation classes is defined by the overall dimensions of the lattice. For example, Proctor's (14) four by five lattice contains 19 different distance-orientation classes. The numbers of pairs of infected plants occurring in each distance-orientation class are statistically analyzed by a log-linear model. The limitations of ordinary runs or doublet tests are overcome by the distance- orientations method; however, the loglinear model is complex and designed to analyze a four by five lattice, although computer programs could be adapted for varying size lattices.

This paper describes a method of analyzing the two-dimensional spread of incidence of a virus in any size lattice. Vacancies within the lattice neither limit the analysis nor affect interpretation of the

data. We utilize the concept of distance-orientation classes, but the distance between infected plants is defined in terms of horizontal (X) and vertical (Y) units not as the length of the hypotenuse; therefore, our pairs of infected plants are grouped into two-dimensional [X, Y] distance classes. The [X, Y] distance class does not identify the position of an infected plant or plants in the lattice, but refers to the absolute distance between plants within a pair. The number of pairs of infected plants observed in each [X, Y] distance class are directly compared to expected values obtained from plots containing the same numbers of randomly distributed infected plants and to their test statistics generated by computer simulations.

MATERIALS AND METHODS

The incidence of watermelon mosaic virus 2 (WMV 2) in muskmelon (Cucumis melo var. reticulatus) was determined in nine and six experimental plots of 200 plants (10 rows, 20 plants per row) grown in the spring and summer, respectively, of 1984. At weekly intervals, six leaf disks (1-cm diameter) were removed from a minimum of three young leaves on each plant in each plot. A slightly modified ELISA protocol was developed (12) to assay each six-leaf disk sample for WMV 2. The WMV 2 incidence data and data presented by Freeman (5) concerning nettlehead virus disease on hops (Humulus lupulus L.) were subjected to spatial pattern analysis. Comparisons of the analytic methods and results were made between our two-dimensional analysis, Freeman's "queen's case" doublet analysis (5), and ordinary runs analysis (6).

Two-dimensional distance class analysis. The counts of pairs of infected plants in each [X, Y] distance class and the number of possible pairs in that class are calculated by FORTRAN computer programs. All plants within the lattice, defined as the number of columns by the number of rows in each column, are identified by their X and Y coordinates: agronomic rows are assigned X values and would correspond to columns in a lattice; plants within agronomic rows are assigned Y values and correspond to lattice rows or in-column positions in a lattice. Thus, columns of the lattice are equivalent to rows in an agronomic field situation and rows of the lattice are equivalent to an across-rows direction in an agronomic field. Each plant is also assigned a status code of 1, 2, or 3 which identifies the plant as healthy, infected, or missing (vacancy), respectively. The status codes are assigned to positions

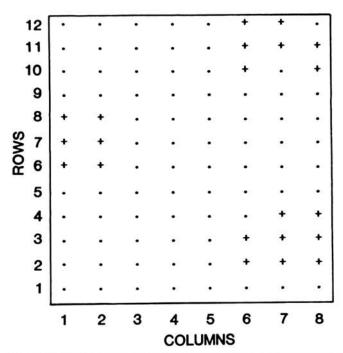


Fig. 1. Spatial patterns of infected plants in an eight-column by twelve-row lattice containing no vacancies. Symbols: • = healthy plant, and + = infected plant.

within an array [the lattice] based on their column and row position or [X, Y] coordinates. The [X, Y] distance between two infected plants is obtained from the absolute value differences between their X and Y values. The pair of infected plants is then assigned to a distance class. For example the [X, Y] distance class of [3,2] refers to any pair of plants such that getting from one plant to the other involves counting three units along a lattice row and two units along the lattice column, i.e., is three agronomic rows over and two plants down the row.

All possible pairs of infected plants within the lattice are identified and assigned to a [X,Y] distance class. The actual number of pairs of infected plants in each distance class cannot be directly compared because the total possible numbers of pairs varies between [X,Y] distance classes. The number of pairs of infected plants occurring within each [X,Y] distance class is, therefore, standardized by dividing it by the total number of pairs of living plants occurring within the same [X,Y] distance class. This allows for direct comparison of the standardized count frequency (SCF) values in any [X,Y] distance classes. The SCFs are dimensionless numbers which do not represent the number of pairs of infected plants per se, but do represent the frequency of occurrence of pairs of infected plants in that [X,Y] distance class relative to the number of pairs of infected plants in all other [X,Y] distance classes in the lattice.

The observed SCFs in each [X, Y] distance class are compared to expected SCFs, determined when the same number of infected plants are randomly assigned locations within a lattice of the same dimensions. Locations of the infected plants in the lattice are generated by a pseudo-random function (9). Vacancies observed in the field are assigned the same fixed X and Y coordinates in the simulations. The SCFs are computed for all [X, Y] distance classes on each of 400 sets of simulator data. The mean SCF and its associated standard deviation for each [X, Y] distance class are calculated. A significance level on the observed SCF for each [X, Y] distance class is computed directly by counting the number of times the simulated SCF exceeds the observed SCF during the 400 simulations. A 95% confidence limit is computed for each significance level by the following equation:

$$CL = (1.96 * (S_{(X,Y)} * (1 - S_{(X,Y)})))/N$$

in which CL = confidence limit, $S_{(x,y)}$ = the significance level of the [X,Y] distance class and N = number of times the simulation was executed.

Example. To illustrate this method a fabricated set of data for an eight-column by twelve-row lattice (Fig. 1) is analyzed by the proposed method. The observed and expected SCFs and their significance levels are presented in Table 1.

The data presented in Fig. 1 may be unrealistic of field data, but the analysis illustrates the power of the two-dimensional distance class tests. Careful scrutiny of the SCF for each [X, Y] distance class and their levels of significance (Table 1) allows identification of the average cluster size and relative location within the lattice. Delimitation of areas of randomly occurring infected plants is also possible. If clusters of infected plants are found in the lattice, their dimensions will be evident from the distribution of the small distance classes (low [X, Y] values) which have SCFs significantly higher ($P \le 0.05$) than expected. There are three ([0,1]; [1,0]; [1,1]) such classes in Table 1 which identifies an average core cluster size of four plants with outer dimensions of one X unit and two Y units.

Two other clusters of distance classes having SCFs significantly higher than expected ($P \le 0.05$) (i.e. ([0,7-10], [1,8-9], [2,8]) and ([5,3-6], [6,3-6], [7,3-5]) represent the relative location of clusters in the lattice. The average distance between clusters is determined by the position of these clusters in the lattice relative to the core cluster in the upper left corner of the lattice. In this example, the distance classes [0,7-10], [1,8-9], and [2,8] indicate that two clusters occur in the same columns, but are separated by five rows in the lattice. The aggregation of distance classes [5,3-6], [6,3-6], and [7,3-5] identifies that a third cluster is separated from the other two clusters by approximately two to three columns and is located between the other two clusters in terms of row position.

Twenty distance classes; [0,3-5], [1,3-6], [2,3-5], [3,0-6], [4,0-1], [5,1]; have SCFs significantly lower ($P \ge 0.95$) than expected. The SCFs for these 20 distance classes indicate that fewer than expected infected plants are located in these distance classes in the lattice, thus providing additional evidence for the presence of clusters of infected plants.

Ordinary runs. Ordinary runs analysis (6) is outlined and explained by Madden et al (11). Each column of the lattice is analyzed separately and results are described as the number of columns in which the infected plants are randomly or nonrandomly distributed.

Although ordinary runs analysis should not be performed with vacancies, we have allowed it to show the advantages of the twodimensional distance class analysis, and have calculated the number of runs in two ways: with the vacancies removed and the remaining plants analyzed, or with the vacancy (or vacancies) treated as a separate run.

RESULTS

The spatial patterns of virus-infected plants resulting from two unrelated field epidemics were each used to compare the spatial pattern analysis techniques. The number and location of plants of C. melo infected with WMV 2 within a 10-column by 20-row lattice (Fig. 2) were analyzed by using the two-dimensional distance class test and ordinary runs analysis. These data are representative of nonpersistent, aphid-borne viruses spread entirely by alate vectors. The pattern of nettlehead disease in hops planted on an 11-column by 30-row lattice (Fig. 3) was analyzed by Freeman (5) who used a two-dimensional doublet analysis. The data were reanalyzed by the two-dimensional distance class test and ordinary runs. Hop nettlehead disease is considered to be caused by an interaction of a strain of Arabis mosaic virus (a nepovirus) with Prunus necrotic ringspot virus (an ilarvirus) (2). The spread of this

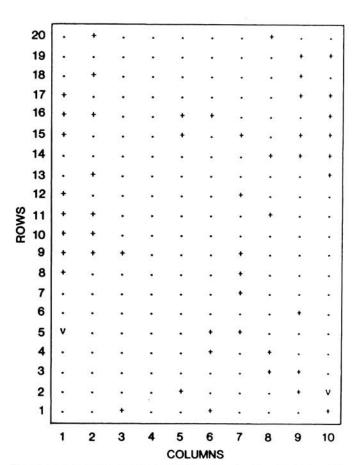


Fig. 2. Spatial pattern of WMV 2-infected muskmelon plants in a 10column by 20-row lattice with two vacancies. Symbols: • = healthy plant, + = infected plant, and v = vacancy.

disease is dependent on the independent dispersal of each virus and on the probability of both viruses successfully infecting the same

The average cluster size of WMV 2-infected plants, determined from the two-dimensional distance class test was indicated by those distance classes with significantly higher SCFs in the upper left corner of Fig. 4, [0,1-3]. The clusters were runs of two to four plants along a column. A significant (P = 0.01) number of diagonally adjacent infected plants were present [1,1]. Whether the significance of the [1,1] class was due to overlapping runs of infected plants in adjacent columns or isolated pairs of diagonally adjacent infected plants cannot be determined. The distribution of clusters, relative to one another, was identified from the pattern of all other distance classes with significantly higher ($P \le 0.05$) SCFs. The aggregation of 24 significant distance classes (i.e., [7,4-8], [8,0-10], [9,0-5], [9,7], [9,9]) (Fig. 4) indicates a majority of the

TABLE 1. Results of the two-dimensional [X, Y] distance class analysis on the hypothetical data. Bold type indicates classes which have a significantly higher ($P \le 0.05$) number of observed infected pairs of plants. Italicized classes have a significantly lower ($P \ge 0.95$) number of observed infected pairs of plants

Line 1.	Standardized number of observed infected pairs of plants.
Line 2.	Standardized number of expected infected pairs of plants.
Line 3.	Level of significance.

	X									
Y	0	1	2	3	4	5	6	7		
0	0.0000	0.1310	0.0556	0.0000	0.0000	0.0000	0.0000	0.0000		
0	0.0000	0.0478	0.0443	0.0454	0.0455	0.0471	0.0443			
0	0.0000	0.0000	0.1825	0.9750	0.9575	0.8775	0.7050			
1	0.1477	0.1039	0.0455	0.0000	0.0000	0.0000	0.0000	0.0000		
1	0.0473	0.0470	0.0472	0.0465	0.0470	0.0467	0.0466	0.0486		
1	0.0000	0.0000	0.4350	0.9975	1.0000	0.9675	0.8550	0.6350		
2	0.0625	0.0500	0.0167	0.0000	0.0125	0.0333	0.0750	0.1000		
2	0.0471	0.0459	0.0451	0.0455	0.0465	0.0465	0.0456	0.0490		
2	0.1450	0.3175	0.9475	0.9875	0.9400	0.8000	0.1175	0.0975		
3	0.0000	0.0000	0.0000	0.0000	0.0417	0.1111	0.1944	0.2222		
3	0.0452	0.0455	0.0475	0.0446	0.0468	0.0456	0.0472	0.0439		
3	0.9800	0.9975	0.9975	0.9925	0.4600	0.0225	0.0000	0.0100		
1	0.0000	0.0000	0.0000	0.0000	0.0781	0.2083	0.3125	0.3125		
1	0.0466	0.0455	0.0467	0.0452	0.0466	0.0467	0.0477	0.0467		
8	0.9750	1.0000	0.9850	0.9675	0.1525	0.0000	0.0000	0.0000		
5	0.0000	0.0000	0.0000	0.0000	0.0714	0.1905	0.2500	0.2143		
5	0.0462	0.0459	0.0465	0.0457	0.0472	0.0437	0.0454	0.0407		
5	0.9550	0.9925	0.9975	0.9800	0.2350	0.0000	0.0000	0.0000		
5	0.0208	0.0238	0.0139	0.0000	0.0417	0.1111	.01250	0.0833		
)	0.0450	0.0474	0.0462	0.0461	0.0442	0.0441	0.0448	0.0481		
,	0.9275	0.9550	0.8750	0.9675	0.3725	0.0300	0.0200	0.4475		
	0.1000	0.0714	0.0500	0.0000	0.0000	0.0000	0.0000	0.0000		
'	0.0459	0.0450	0.0465	0.0442	0.0442	0.0445	0.0437	0.0477		
	0.0150	0.1875	0.2750	0.9025	0.8800	0.7875	0.6200	0.3975		
	0.1875	0.1429	0.1042	0.0000	0.0000	0.0000	0.0000	0.0000		
3	0.0438	0.0458	0.0481	0.0458	0.0471	0.0493	0.0423	0.0450		
3	0.0000	0.0000	0.0715	0.8850	0.8275	0.7525	0.5325	0.3275		
)	0.2083	0.1667	0.0833	0.0000	0.0000	0.0000	0.0000	0.0000		
)	0.0480	0.0459	0.0472	0.0470	0.0496	0.0475	0.0429	0.0450		
)	0.0050	0.0025	0.2375	0.7625	0.7325	0.6050	0.4100	0.2450		
0	0.1250	0.1071	0.0417	0.0000	0.0000	0.0000	0.0000	0.0000		
0	0.0453	0.0492	0.0460	0.0432	0.0456	0.0446	0.0450	0.0394		
10	0.0250	0.1700	0.3100	0.5850	0.5375	0.4300	0.3000	0.1450		
1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000		
1	0.0406	0.0425	0.0417	0.0437	0.0428	0.0383	0.0394	0.0512		
11	0.2825	0.4300	0.3800	0.3475	0.2950	0.2075	0.1400	0.1000		

runs or clusters of WMV 2-infected plants were dispersed throughout columns 1-3 and 8-10 of the lattice. The [X, Y] distance classes having observed SCFs significantly lower ($P \le 0.95$) than expected (i.e. [2,0-3],[2,4-5],[3,0-1],[3,3],[4,2-3],[4,5]) reinforce the conclusion that clustering of infected plants was limited to the columnar edges of the lattice (Fig. 4).

Ordinary runs analysis (vacancies are ignored) of the WMV 2 incidence data (Fig. 2) resulted in columns one (8 of 19 plants infected, 5 runs) and ten (7 of 19 plants infected, 6 runs) containing a nonrandom distribution of WMV 2-infected plants (P = 0.009 and P = 0.046, respectively). The probability of a nonrandom distribution of infected plants in the remaining columns was greater than 0.2 with the exception of column five (P = 0.074). If vacancies were treated as a separate run, the probability of a nonrandom distribution of infected plants in column one (7 runs) and ten (6 runs) becomes 0.067 and 0.095, respectively.

Two-dimensional distance class analysis of the incidence of nettlehead disease (Fig. 3) did not reveal a discrete, average cluster size, but does provide information on the orientation and relative locations of diseased plants. Thirty-eight of the 62 distance classes in the range of X values from 0 to 8 and Y values from 0 to 6 have SCFs significantly higher $(P \le 0.05)$ than expected (Fig. 5).

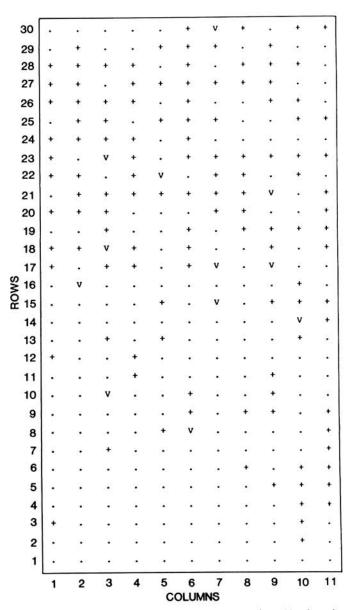


Fig. 3. Spatial pattern of nettlehead-diseased hop plants in an 11-column by 30-row lattice with 12 vacancies. Symbols: \bullet = healthy plant, + = infected plant, + = vacancy.

Conversely, 80 of the 126 distance classes in the range of X values from 0 to 6 and Y values from 11 to 28 have significantly lower ($P \ge 0.95$) SCFs than expected. These findings are consistent with the observation that the majority of the virus-infected plants are at one end of the field. In addition, they provide a quantitative description of the spatial relationship of the infected plants. There is a significantly greater incidence of infected plants along columns, along rows, and diagonally between rows and columns than expected under a random distribution. The original focus (foci) of disease is not apparent, but members of a cluster are confined to within five or six units. The significant distance classes, [9,20–23] and [10,18–20] also indicate that an isolated cluster(s) of infected plants occurs near a columnar edge of the field at the opposite end from where the majority of disease is present.

Ordinary runs analysis of the distribution of nettlehead disease in hops (vacancies are ignored) indicated that column two (10 of 29 plants infected, 7 runs), column four (11 of 30 plants infected, 9 runs) and column six (14 of 29 plants infected, 8 runs) contain a nonrandom distribution of infected plants (P = 0.009, P = 0.037 and P = 0.011, respectively). The significance levels for the remaining columns ranged from P = 0.11 to 0.99. If vacancies are treated as a separate run, the distribution of infected plants in column two (9 runs) becomes random (P = 0.063).

Results of the doublet analysis indicates a significantly greater (P = 0.006) number of infected doublets were observed than expected under the null hypothesis of random distribution.

DISCUSSION

The two-dimensional distance class test has provided a quantitative description of the spatial distribution of WMV 2-infected C. melo and nettlehead-diseased hop plants. WMV 2-infected plants tended to occur in short runs along columns and

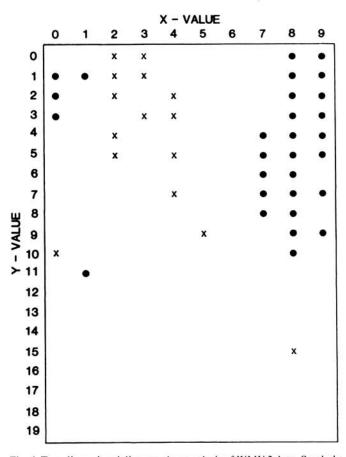


Fig. 4. Two-dimensional distance class analysis of WMV 2 data. Symbols: $\bullet = [X, Y]$ class with a standardized count frequency greater than expected, P = 0.05; $\mathbf{x} = [X, Y]$ class with a standardized count frequency lower than expected, $P \le 0.05$.

were concentrated in columns 1-3 and 8-10. Runs analysis identified nonrandomness only in columns one and ten and cannot quantitatively identify the size of clusters. The distribution of nettlehead disease was concentrated at one end of the lattice. Clusters of infected plants were defined by small unit distances which occurred along columns and rows and diagonally between columns. Although ordinary runs and doublet analysis both identified the occurrence of the nonrandom distribution (clusters) of infected plants, neither analysis provides any information as to the size or shape of individual clusters or the number of clusters or the distance and orientation between clusters.

The ability to identify the spatial pattern of plant populations by distance sampling has long been recognized (3). The direct use of distance measurements or nearest-neighbor analyses (3,13) is restricted by the fact that these methods require an estimate of population density and assume the individuals within the population are randomly distributed. Plants grown in agronomic situations are generally uniformly distributed in rows. The violation of the random distribution assumption confounds the results of these analyses. Nearest neighbor, ordinary runs, and doublet analysis are all acceptable tests for randomness of individuals within a population; however, they do not quantitatively describe the spatial patterns of healthy or infected plants or of the pathogen.

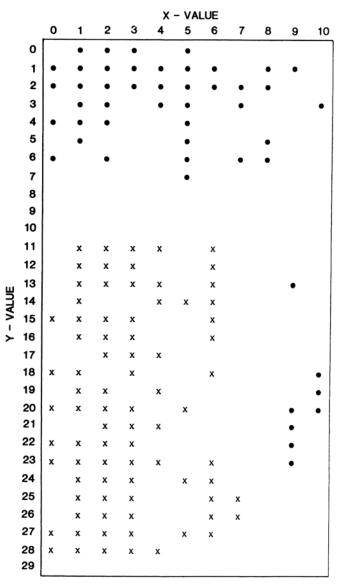


Fig. 5. Two-dimensional distance class analysis of nettlehead diseased hop plants. Symbols: $\bullet = [X, Y]$ class with a standardized count frequency greater than expected, P = 0.05; $\mathbf{x} = [X, Y]$ class with a standardized count frequency lower than expected, $P \le 0.05$.

The two-dimensional distance class method uses a coordinate system with each plant assigned an [X, Y] point in a lattice. The distance relationship between plants, defined by X and Y units or distance classes, can then be used to define the randomness of infected plants occurring within a lattice, the orientation of infected (healthy) plants (ie. down rows, across rows, and diagonally), the distance between individuals within a cluster, and the position of the clusters relative to one another. The comparison of SCF values by Student's t-test allows for comparative analyses of spatial distribution among or within fields at various times.

A quantitative assessment of the spatial pattern of infected plants throughout the epidemic can provide insight into the biology of the pathosystem. Insect-vectored pathogens may enter a field in a random pattern or be influenced by a directional (e.g., wind) (8) or edge effect (10). The dispersal from initial foci may lead to random or clustered patterns of disease. Insect vectors are capable of multiple infections, therefore primary or secondary dispersal by a single aphid may result in small clusters. The occurrence and importance of these types of dispersal can be identified from the spatial pattern data provided by the two-dimensional distance class method. The two-dimensional analyses of the spatial pattern of WMV 2-infected plants indicated a definite edge effect, and clusters of two to four plants concentrated at the edge of a field is an expected type of pattern for an aphid-borne nonpersistent virus if the source of the virus was from an adjacent area (7). One of the viruses associated with the nettlehead disease, Arabis mosaic virus, is nematode transmitted, therefore the spread of this disease is limited by the dispersal and activity of its vector. Plant-parasitic nematodes typically have a patchy distribution and a limited dispersal capability (1). The spatial pattern of nematodetransmitted viruses would be expected to mimic the spatial pattern of its vector and the results of the two-dimensional distance class analysis indicates that the infected plants were clustered and the dispersal of the disease was limited.

The two-dimensional distance class method was designed to ascertain the spatial pattern of individual objects from maps of fields which have been produced frequently at great expense. The method is based on binomial data (e. g., individual plants as sample units), therefore it would not be applicable for evaluating disease severity data or count data. The method is applicable in the spatial evaluation of any disease whose incidence is measured using a binomial classification (i.e., infected or healthy) of individual plants. There are no limitations on the size of the field (lattice) to be analyzed, but computer costs may become unrealistic if the lattice area exceeds 1000.

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