Nonrandom Spatial Distribution of Aphid-Vectored Maize Dwarf Mosaic

GENE E. SCOTT, Supervisory Research Agronomist, Crops Science Research Laboratory, Agricultural Research Service, U.S. Department of Agriculture, and Professor of Agronomy, Mississippi State University, Mississippi State 39762

ABSTRACT

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Ordinary runs analysis was used to determine if plants of corn (Zea mays) with maize dwarf mosaic (MDM) were randomly distributed within the row. Hybrid B had at least twice as many MDM-diseased plants as hybrid A. In 1982 and 1983, the distribution of diseased plants was nonrandom, and the extent of nonrandomness was greater for hybrid B than for hybrid A. The distribution of disease in rows of 50, 100, 200, and 400 plants was compared with simulated data generated with given probabilities for a diseased plant to follow a healthy plant (pHD) and for a diseased plant to follow a diseased plant (pDD). The observed frequency of pDD was 0.15 greater than pHD for hybrid B in both years but somewhat less for hybrid A. Because aphids are the distributors of maize dwarf mosaic virus in the field, the likelihood of aphids carrying the virus to adjacent plants is 15% greater than to nonadjacent plants.

Additional key words: disease spread, epidemiology

Knowledge of the type of disease distribution and spread in a field is critical in epidemiological studies as well as in analysis of yield reduction. Scott and Rosenkranz (7) found that maize dwarf

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mosaic (MDM)-diseased plants adjacent to healthy plants yielded less than when adjacent to other diseased plants. If the distribution of diseased plants is random, the pathogen is not spreading to adjacent plants; however, if the pathogen spreads to adjacent plants, the diseased plants are clustered

Various methods have been used to determine if diseased plants occur at random or in groups within a field. Vanderplank (8) proposed doublet analysis as a technique to determine how the pathogen spreads in field plots. Converse et al (1) suggested that the equation for calculating the standard deviation in Vanderplank's doublet analysis was incorrect and presented a

corrected form of doublet analysis as derived from the work of Freeman (2). Gibbons (4) proposed an ordinary runs analysis to determine random or nonrandom distribution. Madden et al (6) compared ordinary runs, ordinary doublets, and corrected doublets for the distribution of sweet corn plants showing maize dwarf mosaic virus (MDMV) symptoms in the field. They concluded that the ordinary runs was the best of these three tests to determine randomness of diseased plants.

Gibbons (4) has defined ordinary runs as follows: "In any ordered sequence of some two types of symbols, a run is defined as a succession of one or more identical symbols, which are followed and preceded by a different symbol or no symbol at all." Consider that the following pattern of 10 numbers is represented in a row with 10 plants: 2,2,1,1,2,2,1,2,2,2. The 1s represent disease-free plants and the 2s represent disease-free plants. There are five runs in this ordered sequence. Reading from left to right, the ordinary runs are: 22, 11, 22, 1, and 222.

Madden et al (6) give the analysis for ordinary runs. Briefly, the number of diseased and total plants are used to calculate the expected number of runs [E(U)] and the standard deviation. The observed number of runs will be *less* than

E(U) if there is a clustering of infected plants (4). The asymptotic sampling distribution of Z_u is the standard normal distribution (3,4). The value of Z_u (observed number of runs minus the expected number of runs divided by the standard deviation) will be a large negative number if there is clustering. Therefore, the test for nonrandomness (clustering) is one-sided and the left-tail probability is used (4). A row of plants was considered to have a nonrandom sequence of infected and healthy plants if $-Z_u$ was greater than 1.64 (P = 0.05).

This study was conducted to determine if the distribution of MDM-diseased corn plants was random or clustered and compare simulated with actual disease distribution to draw inferences regarding the movement of virus-carrying aphids in the field.

MATERIALS AND METHODS

A commercial hybrid, Pioneer Brand 3369A (hybrid A), was grown in 1981, 1982, and 1983, and a more susceptible commercial hybrid, Pioneer Brand 3368A (hybrid B), was also grown in 1982 and 1983. The test site was 16.4 m wide (16 rows with 0.97 m between rows) with johnsongrass (Sorghum halepense (L.) Pers.) on each side. Johnsongrass areas 5.1 m long and 16.4 m wide (defined as one range) were also positioned across the test site at 20.4-m intervals. Between areas of johnsongrass, four ranges of corn (64 rows) test material were planted.

In 1981, 16 ranges (256 5.1-m rows) of hybrid A were overplanted and later thinned to 25 plants per row. In 1982 and 1983, two ranges of one hybrid were planted followed by two ranges of the other hybrid. This was repeated three times in 1982 and four times in 1983, giving 90 (only 15 rows per range were planted in 1982) rows in 1982 and 120 rows in 1983. In 1982 and 1983, rows were overplanted but not thinned, and the first 25 plants per row were evaluated.

When the plants were 80-110 cm high, each was evaluated for presence or absence of the mosaic symptoms associated with infection by MDMV. Data were recorded on plants in sequence down the row so that the distribution of

diseased plants could be determined. Two end-to-end 25-plant rows were considered as a 50-plant row, and adjacent 50-plant rows were considered as a 100-plant row. Two adjacent 100-plant rows were treated as a 200-plant row, and two adjacent 200-plant rows were considered as a 400-plant row.

A computer program was written to simulate the distribution of healthy and diseased plants in a row of corn plants when the probability for healthy plants and the degree of clumping of diseased plants are given. The program required an input of the pHD and the pDD. Basically, the computer program created numbers from 1 through 10 at random and then, depending on the probabilities assigned, designated the generated number to be a 1 (indicating a healthy plant) or a 2 (indicating a diseased plant). The program maintained a record of the distribution of the 1s and 2s within the row, and after the desired number of "plants" per row were simulated, it calculated an ordinary runs analysis to determine if random or nonrandom distribution of diseased plants occurred in that row. Rows with any number of plants could be simulated, and any number or repetitions could be conducted. For this study, rows with 50, 100, 200, and 400 plants were simulated with 100 repetitions of each. All data, including the simulated data, were analyzed by the procedure given by Madden et al (6).

RESULTS AND DISCUSSION

The percentage of diseased plants varied with year and hybrid (Table 1). Hybrid B had at least twice as many diseased plants as did hybrid A. The percentage of times the $-Z_u$ value was greater than 1.64 (reject hypothesis for random distribution of diseased plants) is given for both hybrids for rows with different numbers of plants (Table 1). The frequency of rejection of the null hypothesis was usually twice as high for hybrid B as for hybrid A, the one exception being when they were essentially equal for 100-plant rows in 1983.

The MDM-diseased plants were not at random in the field. Additional information on the extent of this nonrandom-

ness of diseased plants can be obtained by comparing actual data with data simulated with known pHD and pDD probabilities. Nonrandomness of distribution of diseased plants will increase as the difference between pDD and pHD increases.

Comparison of actual data with simulated data should indicate the approximate values of pHD and pDD that had been operative in the field. For instance, if the average percentage of diseased plants was about 50 and the frequency of rejection of the hypothesis for random distribution with 50, 100, 200, and 400 plants per row was about 30, 76, 92, and 100, respectively, one could conclude that pHD was 0.4 and pDD was 0.7 (Table 2).

The actual data obtained for hybrid B in 1982 matched the simulated data best for a pHD of 0.4 and a pDD between 0.5 and 0.6. The 1983 data for hybrid B best matched the simulated data with a pHD of 0.5 and a pDD between 0.6 and 0.7. Thus in both years, the pDD in the row was about 0.15 greater than the pHD.

Except for the 400-plant rows, no significant indication of nonrandomness for diseased plants was obtained for hybrid A in 1981. The best agreement of the actual data for hybrid A in 1982 with the simulated data was for a pHD of 0.2 and a pDD of 0.3. The 1983 data for this hybrid best matched expected results based on simulated data assuming values of 0.1 and 0.2 for pHD and pDD, respectively.

The distribution of diseased plants was not random, and thus the method by which the virus is transferred to healthy plants must not occur at random. Knoke and Louie (5) only mention two methods of obtaining naturally infected MDMdiseased plants under field conditions. The predominant method is by aphids carrying the virus and inoculating the plant. The other method is the extremely low amount of seed transmission. The amount of seed transmission is probably of consequence only to the extent of introducing the virus into a new area, and the distribution of seeds carrying the virus can probably be assumed to be at random. Therefore, the distribution of diseased plants in the field must reflect the feeding pattern of those aphids carrying the virus.

Nonrandom distribution of diseased plants could occur because an aphid moves to a plant, infects that plant, moves rather quickly to the next plant in the row, and infects that plant and so forth. That is, one aphid inoculates two or more adjacent healthy plants with the virus obtained from a given source plant that may or may not have been close to the plants that were inoculated. Nonrandom distribution of diseased plants would also occur when an aphid carries the virus from one previously infected plant to an adjacent healthy plant. That

Table 1. Percentage of diseased plants and frequency of rejection of the hypothesis for random distribution of maize dwarf mosaic-diseased plants for two hybrids in rows of different lengths

Year	Hybrid	Percent diseased plants	Plants per row					
			50	100	200	400		
1981	Α	42	2/128 ^a (2) ^b	2/64 (3)	2/32 (6)	7/16 (44)		
1982	Α	24	4/45 (9)	2/21 (10)	3/12 (25)	2/6 (33)		
	В	41	9/45 (20)	5/21 (24)	5/12 (42)	3/6 (50)		
1983	Α	13	5/64 (8)	5/32 (16)	4/16 (25)	2/6 (33)		
	В	57	10/64 (16)	6/32 (19)	9/16 (56)	6/8 (75)		

^{*}Number of times hypothesis for random distribution of MDM-diseased plants was rejected/total number of rows with a given number of plants per row.

^bNumber in parentheses is percent rejection of the hypothesis that MDM-diseased plants are randomly distributed within the row.

Table 2. Simulated data for percentages of diseased plants and rejection of the hypothesis for random distribution of diseased plants with given probabilities that a diseased plant follows a healthy plant and that a diseased plant follows a diseased plant

Probability		Plants per row									
Diseased plant follows healthy plant	Diseased plant follows diseased plant	50		100		200		400			
		Diseased plants (%)	Ho: ^a reject (%)	Diseased plants (%)	Ho: reject (%)	Diseased plants (%)	Ho: reject (%)	Diseased plants (%)	Ho: reject (%)		
0.1	0.2	11	7	.11	12	11	28	11	51		
	0.3	12	12	12	30	13	66	13	86		
	0.4	14	25	14	64	14	92	14	99		
	0.5	16	46	16	83	17	100	16	100		
	0.6	18	55	18	96	15	98	•••			
	0.7	19	80	•••	•••	•••	•••	•••			
	0.8	20	95								
	0.9	22	99								
0.2	0.3	21	5	23	16	23	36	22	51		
	0.4	24	12	25	42	25	75	25	95		
	0.5	27	27	27	73	27	99	29	100		
	0.6	30	44	30	88	31	100				
	0.7	33	71	35	99						
	0.8	35	88								
	0.9	37	95	•••	•••	•••	•••				
0.3	0.4	33	4	33	12	32	26	34	51		
	0.5	36	14	37	40	37	73	37	95		
	0.6	39	27	40	70	41	98	41	100		
	0.7	44	50	46	96	45	100				
	0.8	46	72	51							
	0.9	50	88								
0.4	0.5	43	4	44	13	44	24	44	45		
	0.6	47	13	49	33	48	72	48	91		
	0.7	52	30	54	76	54	92	53	100		
	0.8	56	45	59	90	60	100				
	0.9	62	64	67	96						
0.5	0.6	54	5	55	19	56	32	55	47		
	0.7	59	11	60	39	61	77	61	98		
	0.8	65	34	68	70	67	93	67	100		
	0.9	68	40	73	77	73	98	72	100		
0.6	0.7	66	7	66	12	66	26	66	50		
	0.8	70	13	72	33	72	65	72	95		
	0.9	76	15	77	60	78	89	79	100		
0.7	0.8	75	3	76	14	76	25	76	38		
	0.9	81	10	82	32	82	62	83	86		
0.8	0.9	87	0	86	5	87	20	87	35		

^a Percentage of rejection of the hypothesis for random distribution of diseased plants.

is, through a series of individual plant inoculations by aphids moving from a diseased to an adjacent healthy plant, clustering of diseased plants could occur. If plants are evaluated only once, data obtained would reflect the sum of the feeding pattern of all aphids carrying sufficient inoculum to inoculate plants from plant emergence until some period of time (roughly I wk because symptoms would need time to develop) before plants are evaluated for presence or absence of disease symptoms.

The lower percentage of diseased plants in hybrid A could indicate nonpreference for feeding by aphids or some degree of resistance to the virus. These hybrids differed in percentage of diseased plants when mechanically inoculated with MDMV (G. E. Scott, unpublished). Thus, the fewer diseased plants in hybrid A most likely indicates

response to the virus rather than differential feeding by the aphids. If I assume that the feeding pattern of aphids was essentially the same for both hybrids, then some plants of hybrid A fed upon by aphids carrying the virus did not become diseased. This would reduce the percentage of diseased plants and probably increase the number of "runs" within the row, which would reduce the frequency of rejecting the hypothesis for random distribution of diseased plants. Hybrid A did have a lower percentage of diseased plants and a lower frequency of rejection of the null hypothesis than was obtained for hybrid B. Thus the relative susceptibility of the hybrid to the virus will influence the estimate of the amount of nonrandomness of the aphid feeding behavior.

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