Distribution of Wheat Powdery Mildew Incidence in Field Plots and Relationship to Disease Severity

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ABSTRACT

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Disease severity and incidence of powdery mildew of wheat were determined each week on individual leaves in quadrats consisting of 10 tillers at 10 randomly selected locations in each of 30 field plots of the winter wheat cultivar Chancellor for 8 wk beginning 28 April 1978. A linear relationship was observed between disease severity on tillers and disease severity on individual leaves throughout the epidemic. Disease severity was logarithmically related to disease incidence on individual leaves and tillers. Disease incidence, the proportion of diseased leaves to total number of leaves examined, did not reach 100% until the end of the season, when disease severities were between 30 and 40%. Relationships between disease incidence and disease severity were determined for leaves at four positions

in the plant canopy. For the first 4 wk of the epidemic, the spatial frequency distribution of disease incidence on leaves was best described by the negative binomial distribution, indicating that diseased leaves tended to be aggregated. The degree of aggregation decreased as the season progressed, and by the fifth or sixth weeks of the epidemic, disease incidence on leaves was randomly distributed. The negative binomial coefficient k or the mean to variance ratio provided a quantitative measure of degree of aggregation in foci. The results of this study are used as the basis for discussing sequential sampling procedures that might improve precision of estimation of disease severity and yield loss for wheat.

Additional key words: epidemiology, Erysiphe graminis f. sp. tritici, sampling, Triticum aestivum

Accurate assessment of plant disease severity, although critical to understanding the epidemiology of plant disease and yield-loss relationships, continues to be a major and often unresolved problem. The use of percentage scales and keys of visual disease severity (percent of leaf covered or affected), remote sensing, and such indirect methods as spore counts and disease incidence (percentage of infected plant units) are considered valid approaches to disease assessment (9). Severity of powdery mildew on small grains has often been estimated visually by a percentage scale method (3,7,8,14). This method involves subjective judgment and introduces an error of unknown magnitude, depending on the judgment of different assessors or of the same assessor at different times. In addition the method may be tedious and time-consuming, two attributes that may affect the assessments.

Estimating disease severity indirectly from disease incidence may reduce some of these problems. Basic knowledge of the relationship between visible disease severity and incidence must be obtained before disease incidence can be efficiently used as a measure of severity.

James and Shih (10) first studied the relationship between disease incidence and visible disease severity for powdery mildew of wheat and leaf rust of wheat. Using disease severity data collected from a large geographical area for each of the top four leaves (top or flag = leaf 1), they found that the relationship between severity and incidence of powdery mildew was described by the model: $S = b \ln(1 - I/100)$, where S = disease severity, I = disease incidence, and b is a constant.

The first objective of our study was to extend the work of James and Shih (10) throughout an epidemic in field plots that could be intensively sampled to determine whether the logarithmic model was appropriate throughout an epidemic and how the severity-incidence relationship changed with time.

A second objective of our research was to determine the spatial distribution of powdery mildew of wheat in field plots and to

describe quantitatively how spatial distribution changed through time. Knowledge of the spatial distribution of disease contributes to understanding the epidemiology of disease, since spatial distribution is determined by components of the disease cycle such as survival, source of primary inoculum, and mode of dissemination. Few quantitative studies of spatial distribution of disease in commercial fields or field plots have been reported (5,6,11,20). Also, the spatial distribution of disease in the field contributes to the magnitude of sampling error in visual disease severity estimates (15).

Strandberg (20) studied the spatial frequency distribution of black rot in cabbage fields and used this information to apply a sequential sampling procedure for estimating disease incidence and to infer the source of inoculum and means of localized dissemination. We discuss the feasibility of using incidence-severity relationships combined with knowledge of the spatial distribution of disease for improving estimates of severity of powdery mildew of cereals, in light of our data.

MATERIALS AND METHODS

Thirty-six 2.5 × 4.5 m plots, each containing 10 rows spaced 17.7 cm apart, were planted with soft red winter wheat (Triticum aestivum L. 'Chancellor') on 28 September 1977, at a seeding rate of 120 kg/ha in a 2.5-ha field. Plots were arranged in a grid with 25 m of the winter barley cultivar Pennrad surrounding each plot to minimize plot interactions. The plots received 200 kg/ha 5:10:10 fertilizer after planting in the fall and 80 kg/ha 34% ammonium nitrate in the spring. Plots were sprayed with 2,4-D at a standard rate the last week of April.

Powdery mildew caused by Erysiphe graminis f. sp. tritici developed in the plots from natural inoculum. Disease readings were made at 7-day intervals for 8 wk beginning 28 April 1978 when plants were at the late tillering growth stage on the Feeke's scale (13). The number of powdery mildew colonies on each leaf and the position of that leaf on the tiller were recorded on 10 consecutive tillers at 10 locations selected at random in each plot each week.

Percentage of leaf area covered by mildew was visually estimated when individual colonies could not be distinguished because of colony coalescence. On and after 25 May 1978, all disease readings were recorded as visual estimates of percentage of leaf area covered by the colonies. Disease records were not made for leaves with extensive necrosis attributable, at least in part, to senescence. Infections on the stems or leaf sheaths were not recorded.

Plant growth was recorded approximately at 10-day intervals by measuring the total leaf area of four tillers selected at random in randomly selected plots. Total leaf area for each leaf on each tiller was obtained by photocopying fresh leaves and calculating their area with a Numonics EGC digitizer (Numonics Corporation, North Wales, PA 19454). Average colony size was estimated in a similar manner and was 2.4 mm^2 with a standard error of 0.7 mm^2. Regression of leaf area for each leaf position over time provided the model that was used to calculate percent disease from counts of colonies (17). This was calculated as the product of number of lesions times 2.4 mm^2 times 100 divided by the size of the appropriate leaf (according to position) as estimated from the regression model. The standard deviation of the predicted leaf area, Y, about the regression for leaf areas of leaves 1 through 4 vs time were 4.1, 3.4, 2.9, and 1.6 cm^2, respectively. Six plots had diminished stands caused by factors other than powdery mildew, and disease severities in these plots were not used in the analysis.

Numbers of lesions per leaf, lesions per tiller, infected leaves per quadrat, infected leaves individually by leaf position in quadrats, and infected tillers per quadrat for the 30 field plots were arranged into frequency classes. The data were analyzed for goodness of fit to several discrete frequency distributions with a FORTRAN IV program developed by Gates and Etheridge (4). Regression analysis (16) was used to examine the relationships between disease severity in the individual plots (measured as an average of ratings from the 10 quadrats) and disease severity on individual leaves by position on the tillers for the plots. Regression analysis was also used to relate disease severity to disease incidence. The appropriateness of specific regression models to describe the data was determined in part by analysis of residual errors using a normal scores test and by examining plots of residuals vs predicted values (16). Regression models were tested by using the F statistic and found to be significant (16).

RESULTS

Powdery mildew was confined primarily to the lower leaves early in the season and progressed to the upper leaves, including the flag leaf, late in the season. The relationship between the average disease severity in each plot and the average disease severity on each leaf by position in each plot was linear each week (Table 1) and the residual errors for each regression were normal. The highest coefficients of determination for each week were most often obtained by comparing average disease severity in the plots with the average disease severity on the third leaf position. The relationship between average disease severity in the plots and severity on each leaf position was strongest on the second and third leaves by the end of the epidemic, as measured by the coefficients of determination (Table 1).

Use of R^2 values and analysis of residuals to compare linear, quadratic, cubic, and logarithmic models led to selection of James and Shih's model (10). Disease severity vs disease incidence on each leaf by position, on all leaves, and on tillers for each week was curvilinear (Fig. 1). The semilog transformation (ln S) with a constant term in the model gave the best fit to the data based on comparison of R^2 values and analysis of residuals. The semilog model, however, does not allow for the fact that disease severity must be zero at zero disease incidence. All other models tested were forced through the origin. The relationship between disease severity and disease incidence for several of the units sampled changed by week (Table 2). The value $z = e^{1/b}$ was calculated for each severity-incidence relationship by week; z is a relative measure of the rate of increase of incidence with increasing severity. The larger the value of z, the faster is the increase in disease severity relative to increasing disease incidence (10). James and Shih (10) observed z values between 0.3 and 0.68 for powdery mildew of wheat. Results from this study showed that z values increased in magnitude from lower to higher leaves at any growth stage (Table 2). As the epidemic progressed temporally, the value of z fluctuated in a random way for each unit sampled with the exception of total leaves where z values fell into one of two groups (Table 2). The first group, represented by the first 4 wk, had z values between 0.829 and 0.851; the second group, representing the next 3 wk, had z values between 0.903 and 0.906 (Table 2). The pooled regression of disease severity vs disease incidence for all leaves gave a reasonably good fit in spite of the two groups (Fig. 1E).

Counts for each of the units sampled in each of the 300 quadrats (ie, infected leaves in quadrats, infected tillers in quadrats, etc.) from all plots combined for each of the first 4 wk of the epidemic were analyzed for goodness of fit to the Poisson, negative binomial, Thomas double Poisson, Neyman type A, Poisson with zeros, and logarithmic with zeros distributions. The negative binomial distribution most satisfactorily described the data when infected leaves constituted the sampling units (Table 3). None of the distributions tested fitted any of the incidence data later in the season than shown in Table 3. Comparison of frequency plots for the latter part of the epidemic indicated no consistent pattern for the distributions of frequencies. The mean to variance ratios of the counts of number of infected leaves (taken separately by leaf position or together) per quadrat tended to increase to values approaching 1.0 or greater as the season progressed (Table 4), indicating that a random distribution might have been expected to fit the frequency of infected leaves in the plots during the latter part of the epidemic (19). This conclusion also was suggested by the increase in the value of k for the negative binomial distribution as

TABLE 1. Linear regression coefficients for the regression of disease severity per field plot against average disease severity on individual leaves during an epidemic of powdery mildew on wheat in 1978

Week	GS[b]	First leaf[a]			Second leaf			Third leaf			Fourth leaf		
		b_o[c]	b_1[e]	R^2[d]	b_o	b_1	R^2	b_o	b_1	R^2	b_o	b_1	R^2
1	5	...	...	...[e]	0.20	11.2	40.9	0.05	0.53	98.2	−0.05	0.32	95.7
2	6	...	...	...[e]	0.55	5.9	12.5	−0.06	0.64	97.1	−0.07	0.31	98.1
3	6–7	1.63	23.6	59.5	0.61	3.8	72.1	0.19	0.57	96.3	−0.08	0.34	93.4
4	7	2.87	9.2	16.8	2.06	1.6	50.6	−0.07	0.63	84.6	0.13	0.32	82.1
5	8	2.77	54.3	45.0	1.25	3.7	90.3	0.02	0.74	99.2	−0.05	0.38	98.2
6	9	6.39	26.1	37.3	0.90	1.8	89.1	0.43	0.66	97.3	−0.13	0.40	92.9
7	10	4.88	4.7	75.6	0.83	1.1	93.2	0.03	0.57	97.6	5.4	0.48	55.3
8	10.1	3.50	3.7	80.2	1.22	0.8	89.7	2.61	0.41	87.4	...	...	...[f]

[a] First leaf is the flag leaf, second is the leaf below the flag leaf, etc.
[b] GS = Growth stage on the Feeke's scale.
[c] b_o is intercept, b_1 is slope.
[d] Coefficient of determination adjusted for degrees of freedom.
[e] No disease present on the first leaf on weeks 1 and 2.
[f] Fourth leaf senesced on many plants by week 8.

the season progressed (Table 3). A smaller value of k reflects greater clustering of infected leaves (1,21). Pielou (18) points out that quadrat size may affect the apparent degree of randomness. Data for colonies on individual leaves had a very low mean to variance ratio, suggesting extreme aggregation of lesions. Although the negative binomial distribution came closest to fitting these data, the probability of exceeding the chi-square value obtained was significant at the 0.01 level. Infected tillers in quadrats fit only the Neyman type A distribution (Table 3).

DISCUSSION

Among the models that we examined, the model of James and Shih (10) best described the relationship between disease severity and incidence of powdery mildew of wheat in our field plots. Our results, however, differed from those of James and Shih (10) in several ways. They used the value $z = e^{1/b}$ from their model to make comparisons between leaf rust and powdery mildew and among leaf positions. We observed consistently higher z values than James
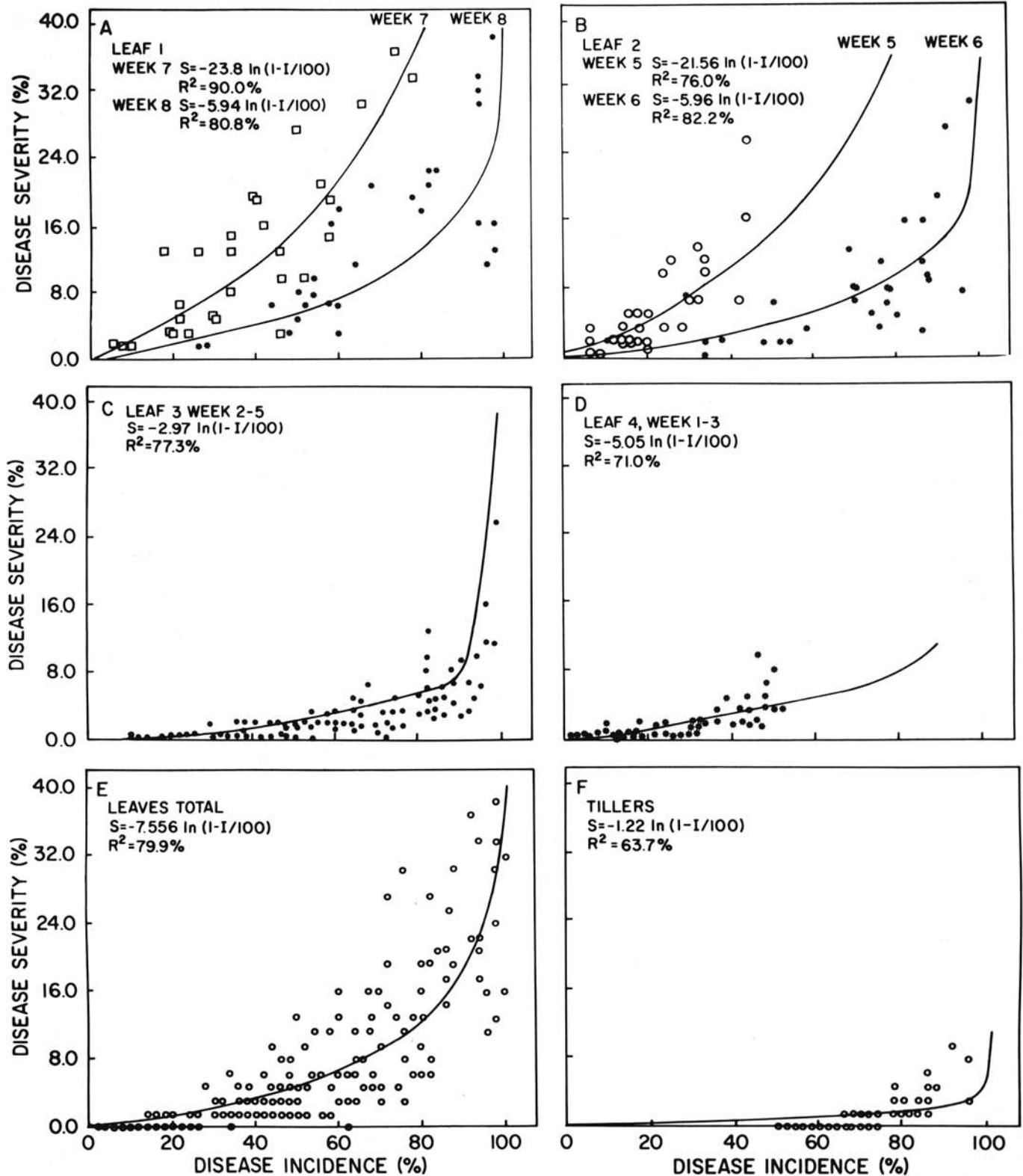

Fig. 1. Incidence vs severity of powdery mildew (*Erysiphe graminis* f. sp. *tritici*) of wheat, fitted to the model $S = b \ln (1-I/100)$. **A**, Leaf 1, weeks 7 and 8; **B**, leaf 2, weeks 6 and 7; **C**, leaf 3, weeks 2–5; **D**, leaf 4, weeks 1–3; **E**, total of all leaves, weeks 1–8; and **F**, tillers, weeks 1–3.

TABLE 2. Coefficients representing the relationship between disease severity and incidence for first through fourth leaves,[w] total leaves, and tillers each week of a powdery mildew epidemic

Week[x]	First leaf		Second leaf		Third leaf		Fourth leaf		Total leaves		Tillers	
	z	b[y]	z	b	z	b	z	b	z	b	z	b
1	...	...	0.95	−18 a	0.55	−1.7 a	0.60	−1.9 a	0.84	− 5.8 a	0.22	−0.67 a
2	...	...	0.93	−14 a	0.64	−2.3 ab	0.59	−1.9 a	0.83	− 5.3 a	0.32	−0.87 a
3	0.99	−102 a[z]	0.93	−15 a	0.69	−2.7 ab	0.64	−2.2 a	0.86	− 6.7 a	0.48	−1.36 b
4	0.99	−95 a	0.93	−13 a	0.61	−2.0 ab	...	...	0.86	− 6.3 a	...	...
5	1.00	−325 b	0.96	−22 a	0.75	−3.4 b	...	...	0.91	−10.1 b	...	...
6	1.00	−224 ab	0.85	−6 b	...	...	...	...	0.91	−10.1 b	...	...
7	1.00	−24 c	...	...	...	...	...	...	0.90	− 9.8 b	...	...
8	0.88	−8 d	...	...	...	...	...	...	0.86	− 6.4 b	...	...

[w] First leaf is the flag leaf, second is the next leaf below the flag leaf, etc.
[x] Week 1 represents 28 April 1978 and week 8 represents 19 June 1978. Weeks 2–7 represent the 7-day intervals between samplings.
[y] The value b was obtained from the regression of percent severity against $\ln(1-I/100)$ where I is percent incidence. The value $z = e^{1/b}$.
[z] Statistical differences calculated using confidence intervals for the regression coefficient and a significance level of $P = 0.05$. Values not showing the same letter are significantly different.

and Shih (10). We interpret this to mean that early in the season the rates of increase of disease severity relative to disease incidence on the third and fourth leaves (growth stages 5 and 6 on the Feekes scale) in our plots were greater than in James and Shih's survey in May 1969 (growth stages 8 and 9). Disease incidence on third and fourth leaves in our study had reached 100% by growth stages 8 and 9. During the season we observed z values as high as 1.00, which is considerably higher than James and Shih's highest value of 0.68 on the second leaf in June. This indicates that the naturally occurring epidemic of powdery mildew in our plots occurred early, possibly with a high level of initial inoculum, and increased more rapidly in severity relative to incidence than did the epidemics in Ontario in 1969 and 1970.

Values for z in the earlier study (10) were lower on the upper leaves than on lower leaves, but our results show an opposite trend (Table 2). James and Shih (10) speculated that higher relative humidity low in the canopy and higher nitrogen levels in lower leaves might be responsible for the greater increase in disease severity relative to disease incidence on lower leaves. Relatively cool humid conditions in our plots early in the season, combined with high levels of initial inoculum, subsequent incoming inoculum, or the cultivar we used, may explain our results.

We were interested in how the disease incidence-disease severity relationship might change as the season progressed. Values of z changed significantly for total leaves in quadrats coinciding with flag leaf emergence during weeks 4 and 5, and the value of z for total leaves and the first leaf decreased the last week that disease estimates were made (Table 3); otherwise, our results did not indicate a particular trend in z values during the epidemic (Table 2).

The frequency distributions of disease observed during the first 3 or 4 wk of the epidemic imply that discrete foci resulted from nonrandom deposition or colonization by primary or secondary inoculum early in the season. The relative degree of aggregation can be measured by the parameter k (Table 3). Small values of k (<1) indicate extreme aggregation of diseased units; larger values indicate a smaller degree of aggregation (20). The k values in our study indicate a trend toward less aggregation, ie, toward randomness as the season progressed. Thus, in our field plots powdery mildew progressed from distinct foci (indicated by small k values) to more random distribution throughout the plots as a result of dispersion of inoculum. Since the negative binomial distribution can be derived from a wide variety of chance mechanisms (2) leading to aggregation of sampling units and since we did not measure dispersion, our interpretation of the observed change in k, although reasonable, is hypothetical.

A second measure of aggregation is the mean to variance ratio. Random distribution of disease among sampling units in a field plot should be characterized by a mean to variance ratio approximating 1.0. The epidemic was initiated from aggregations or foci of infected units; subsequent disease spread led to less aggregated foci until the fourth or fifth week of readings when distinct foci had disappeared and disease appeared to be randomly

TABLE 3. Selected distributions for sampling units (leaf positions) for the early part of a powdery mildew epidemic of wheat

Sampling unit in quadrat[a]	Week[b]	Distribution	k	Mean	Variance	$P > X^2$
Infected tillers	1	Neyman type A	...	3.39	9.08	0.29
	2	Neyman type A	...	4.87	27.64	0.13
Infected second leaves	1	Negative binomial	0.33	0.31	0.58	0.037
	2	Negative binomial	0.25	0.39	0.91	0.746
	3	Negative binomial	0.70	1.45	3.09	0.128
	4	Negative binomial	1.09	2.07	4.84	0.001
	5	Negative binomial	1.81	2.27	4.66	0.229
Infected third leaves	1	Negative binomial	1.15	2.52	6.95	0.084
	2	Negative binomial	1.93	3.74	9.16	0.005
Infected fourth leaves	1	Negative binomial	0.81	1.56	4.03	0.155
	2	Negative binomial	1.73	2.44	5.19	0.007
	3	Negative binomial	5.43	3.57	5.56	0.017
Infected leaves	1	Negative binomial	0.93	4.39	21.50	0.411
	2	Negative binomial	1.68	6.59	27.64	0.054
	3	Negative binomial	3.37	10.29	36.11	0.019
	4	Negative binomial	18.31	13.37	38.01	0.003
Colonies on leaves	1	Negative binomial	0.05	0.75	10.23	0.004
	2	Negative binomial	0.08	0.90	10.04	0.002

[a] Quadrats contained 10 consecutive tillers in a single row.
[b] Week 1 coincides with 28 April 1978.

distributed. Just as the increase in the value of k documents this trend, so does the temporal change in the mean to variance ratio (Table 4).

Assuming that the field plots were relatively uniform and that colonization by *E. graminis* f. sp. *tritici* did not differ significantly among plots, the temporal change in spatial distribution reflects the pattern of inoculum dispersal. Random dispersion of inoculum should lead to random distribution of disease among sampling units in a field plot characterized by a mean to variance ratio approximating 1.0. Since mean to variance ratios for infected
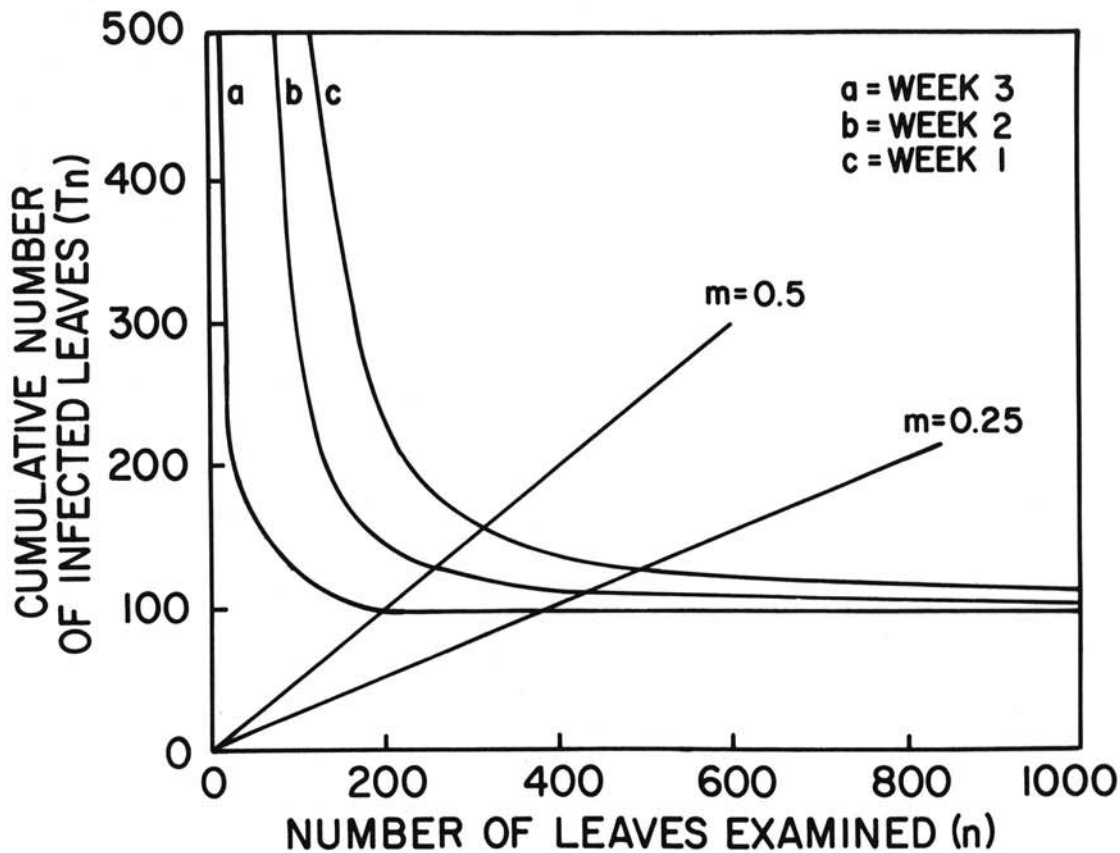
Fig. 2. Sampling curves (stop lines for sequential sampling) for estimating the average number of plants infected by powdery mildew (*Erysiphe graminis* f. sp. *tritici*) in a population with theoretical means (m) equal to 0.5 and 0.25 (50 and 25% of the leaves infected) for: **C**, week 1; **B**, week 2; and **A**, week 3 of a powdery mildew epidemic in 30 field plots of winter wheat cultivar Chancellor.

TABLE 4. Mean to variance ratios for sampling units (leaf positions) for weekly counts of powdery mildew disease incidence on wheat in 1978 field plots of the cultivar Chancellor

Week[b]	GS[c]	Infected leaves in quadrats[a]			
		Second leaf	Third leaf	Fourth leaf	Total all leaves
1	5	0.53	0.36	0.39	0.20
2	6	0.43	0.41	0.47	0.24
3	6–7	0.47	0.57	0.64	0.29
4	7	0.43	1.22	0.68	0.35
5	8	0.49	1.06	1.04	0.69
6	9	1.33	1.32	⋯	0.66
7	10	1.38	⋯	⋯	0.85
8	10.1	⋯	⋯	⋯	0.92

[a] Quadrats contained 10 consecutive tillers in a single row.
[b] Week 1 coincides with 28 April 1978. Sampling after that date was done at 7-day intervals.
[c] GS = Growth stage on the Feek's scale.

leaves in quadrats early in the season were significantly less than 1.0, a plausible inference would be that the gradient of dispersal of inoculum led to substantial deposition within foci early in the season, but as the epidemic progressed, dispersal of inoculum throughout the plots led to a faster increase in disease incidence and severity in areas between foci than within foci.

Improved sampling methods are needed in epidemiology. James (7) suggested that disease incidence data might be used to indirectly estimate disease severity. Our results, when compared with James and Shih's, indicate a variable relationship between disease severity and disease incidence for powdery mildew of wheat and lead us to conclude that powdery mildew incidence may be a poor indicator of powdery mildew severity unless adjustments in the disease severity-disease incidence relationship are made to account for environmental factors that cause the relationship to change from year to year or place to place.

Strandberg (20) used the fact that black rot of cabbage was negative binomially distributed to devise a sequential sampling procedure (12) that allowed calculation of sample size needed to obtain an estimate of disease with a given level of precision. Using our data for incidence on leaves regardless of position and our estimated fit to the negative binomial distribution, we constructed a sampling curve (Fig. 2) similar to Strandberg's. If we were to sample sequentially until we had a large enough sample to be precise within 10% of the mean when the mean (m) was approximately 0.25 (expressed as proportion of infected sampling units), we would need to sample 500 leaves on week 1 and 400 leaves on week 3 (Fig. 2). Further, if disease incidence between weeks 1 and 3 had increased to m = 0.5, we would have needed to sample only 200 leaves to be as precise as we were on week 1 when we sampled 500 leaves (Fig. 2). This example indicates the potential importance of gaining knowledge of the spatial distribution of disease and its change over time.

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