Gradients in Horizontal Dispersal of Cereal Rust Uredospores

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ABSTRACT

Gradients of uredospore dispersal for *Puccinia graminis* f. sp. *tritici*, stem rust, and *P. recondita*, leaf rust, were determined within and around a 72-m-diam source plot of wheat, *Triticum aestivum* 'Lee'. Spore samples were obtained using 5-mm-diam rod impaction traps 15 cm above the crop canopy stationed on annuli inside and outside the plot. No gradients in numbers of spores/cm^2 occurred between annuli inside the source 9 or more m. Numbers of spores on the downwind axis inside the plot increased within the first 9 m from the upwind edge of the source to 80 to 90% of the number trapped over the downwind edge of the source. Gradients outside the source differed with the methods of expression. The greatest gradient in numbers of spores was observed when the gradient was expressed as the average trapped at each annulus. This gradient predicts that an average of 3 and 6% of the initial number of spores trapped over the source will be trapped at 100 m, for stem and leaf rust, respectively. The regression equation of the form $\log \hat{Y} = \log a + b \log X$ approximately described these gradients to an annulus. The omnidirectional horizontal gradient calculated from the sum of the spores per unit width at annuli 36 and 72 m from the source compensated for horizontal dilution as the circumference of the annuli increased with distance from the source. This calculation showed that 14 and 24% of the initial number of stem and leaf rust spores, respectively, were still in this horizontal plane at 100 m. The gradient for the number of uredospores/cm^2 downwind from the source showed that 10% of the spores of each rust species reached a point 100 m downwind. The regression equation of the form $\log \hat{Y} = \log a + bX$ described the downwind movement of both rust species.

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Rapid increase of disease in cereal rust epidemics is partly due to the large numbers of uredospores which may be produced at each infection site, and to the effectiveness of these uredospores as dispersal units. The interaction of host susceptibility, pathogen virulence, and host growth stage, within the limits of the environment, determine the rate of disease increase and, consequently, epidemic development. However, the development of epidemics, over wide areas, ultimately depends on spore dispersal. The importance of spore dispersal in epidemic development has long been recognized, but most of the information on spore dispersal gradients is deduced either from studies of particle movement in the air or from more general studies of disease spread.

Chamberlain (3), Gregory (4, 5), and Schrödter (13) have developed theories on spore dispersal derived from (i) the movement of spores and particles in relatively short wind tunnels; (ii) the dissemination of spores released from point sources in the field; (iii) the study of plant disease gradients; and (iv) the consideration of the physical laws of particle movement. Although these theories may properly describe actual gradients from natural sources of inoculum, empirical evaluation is lacking. Each of these theories is limited by the nature of the data utilized. Wind turbulence, a most important factor in the field, is minimal in wind tunnels. Spore dispersal gradients from point sources are known to be steeper than those from area sources (6). Plant disease gradients of the cereal rusts are not only dependent on spore dispersal gradients, but also on host susceptibility and favorable environmental conditions, which are often a greater limitation than spore dispersal gradients. Gradients of uredospore dispersal calculated from physical laws of particle movement assume a constant shape and mass for the spores, but these characteristics are known to change under variable conditions of temperature and humidity (14). Thus, a question exists about how well the theories of spore movement describe the actual field situation. Furthermore, no theoretical gradients have been developed that apply to conditions within the spore source.

The empirical characterization of horizontal dispersal gradients is relevant to evaluation of control measures such as isolation, sanitation, field resistance, and experimental plot design for epidemiological studies. In the present study, I determined the horizontal dispersal of cereal rust uredospores in and near the area of their production by means of impaction traps. These observed gradients of spore dispersal in the field were compared with those obtained by theoretical models for the prediction of uredospore movement.

MATERIALS AND METHODS.—A circular plot of wheat, 72 m in diam, planted in the center of a square field of 4 hectares, served as the uredospore source. Spring wheat (*Triticum aestivum* L. 'Lee') susceptible to the prevalent forms of stem and leaf rust was used in the plot. The field surrounding the plot was planted to barley (*Hordeum vulgare* L. 'Larker') to provide a surface aerodynamically similar to that of wheat. Larker was thought to be resistant to the prevalent forms of stem rust (*Puccinia graminis* Pers.) occurring in the area.

To assure an adequate production of stem rust uredospores, the wheat was uniformly inoculated

(12) with *P. graminis* Pers. f. sp. *tritici* Eriks. & E. Henn., race 15B-2. Early natural infection of *P. recondita* Rob. ex Desm. made inoculation with leaf rust unnecessary. On 6 July, both stem and leaf rust (*P. graminis* f. sp. *tritici* and *P. hordei* Fckl., respectively) were discovered on the barley. Rust prevalence on the barley was approximately one pustule of each species/100 culms. Therefore, the barley was mowed on 8 July to remove this source of spores. The barley had dried sufficiently so that no green tissue remained by the afternoon of 10 July. Uredospore numbers were obtained and analyzed for the period 11 July through 6 August. The rust severity was one pustule/100 culms for each rust species on 11 July, and increased to 80% severity for leaf rust on 25 July and 80% severity for stem rust on 3 August.

Spore trapping stations were located at the center of the wheat plot and on concentric rings with radii of 9, 18, 27, 36, 72, and 108 m (Fig. 1). Thus, the

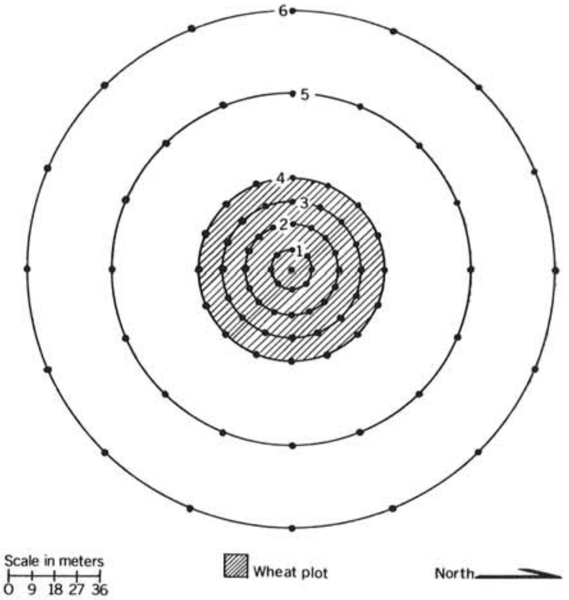

Fig. 1. Location of uredospore trapping stations within and around a 72-m-diam wheat plot.

center station and the inner three concentric rings, each with eight trap stations, were inside the wheat plot. Rings 5 and 6 contained 16 traps each and were located in the field originally planted to barley. A single 5-mm-diam rod impaction trap (10) was located at each station on a wind vane attached to a pole of adjustable height. The traps were maintained 15 cm above the crop canopy. Thus, the traps sampled spore distribution throughout the season in a horizontal plane at a fixed distance above the crop canopy. The traps over the barley stubble were maintained at the same height as those in the wheat field. Traps were placed in the vanes shortly after 0800 and removed shortly before 1700 daily, from 26 June through 6 August 1967. The trap in the center of the wheat plot was replaced at 1700 hr so that this station was operated 24 hr a day to test the adequacy of the sampling period. The impaction traps were processed and spores counted in the manner previously described (10). The nearest significant source of exogenous uredospores was ca. 0.4 km northeast of the northeast corner of the test area.

RESULTS.—The daily number of uredospores (9) of each rust species impacted on the vertical rod traps in and around the area source was obtained. Calculations were made with the data collected after 11 July to eliminate the spurious effects caused by rust infection in the barley prior to this date.

Comparatively few spores were trapped at the station in the center of the wheat plot from 1700 to 0800 hr, except for stem rust uredospores on 1 and 3 August. The regression of the cumulative spore counts on time also were similar for the 24-hr station and those stations inside the plot operated during the day. Thus, the active period of spore dissemination was effectively sampled from 0800 to 1700 hr.

The average number of uredospores/cm^2, impacted during the season on the leading edge of rod impaction traps located on each concentric ring about the center of the spore source, is shown in Table 1. The totals are the sums of the daily number of uredospores trapped during the period 11 July through 6 August. The spore number of each rust species, their fiducial limits, $t_{.05}s_{\bar{x}}$, and the coefficients of variation suggest that traps located within the spore source were sampling one population, whereas traps at the edge of and outside of the source plot were sampling populations with different means.

Analyses of variance were used on the spore count data for each rust species to ascertain if a significant difference existed between the numbers of uredospores trapped in the concentric rings of traps. The variance ratio, *F*, was obtained for the cumulative spore number of each rust species along with the daily spore number for each rust species. The *F* values from analyses of data for stations on rings inside the plot 9 m or more were not significantly different at the .01 level, with one exception, a daily spore count for stem rust which was significant at the .05 level. The *F* values were significant both when data from ring 4, or rings 4, 5, and 6 were included with the data collected within the source. These tests then substantiated the existence of differences in population means inside and outside the source plot. Furthermore, it was concluded that numbers of uredospores impacted on 5-mm-diam rods were not greatly different at stations inside the wheat plot on the annuli at 9, 18, 27, or 36 m, and that no gradient occurred between these annuli.

Uredospore gradients parallel to the wind direction.—The apparent downwind direction was defined as the axis on which the station had the largest number of spores in rings 4, 5, and 6 on one side, and the smallest number of spores in these rings on the opposite end of the axis. This estimation of the downwind direction was required because shifts

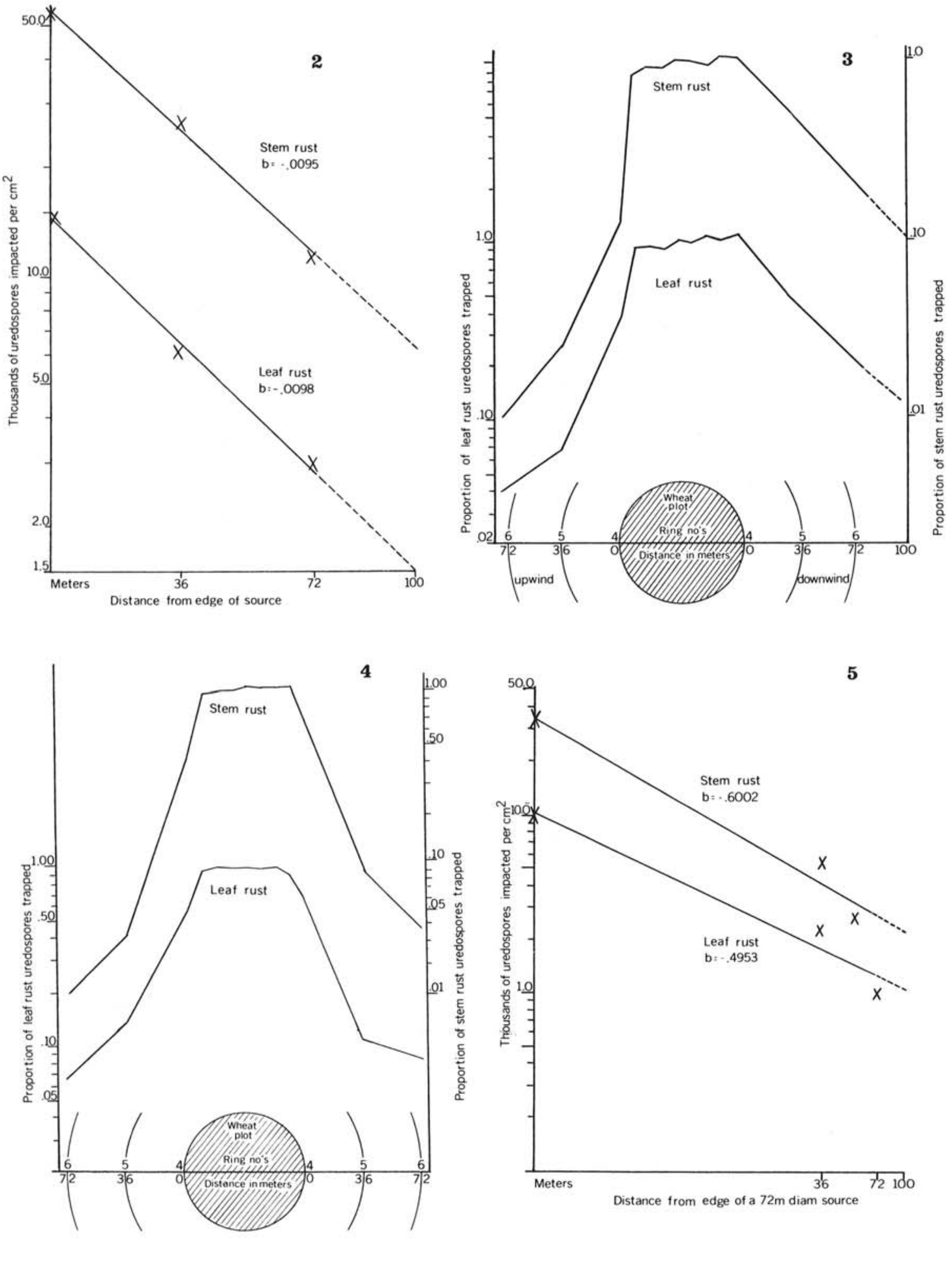

Fig. 2-5. 2) Uredospore dispersal gradients for the mean cumulative numbers of spores trapped in the source and at 36 and 72 m downwind. **3)** Gradients of horizontal dispersal of cereal rust uredospores along the axis parallel to wind direction across the experimental area. **4)** Gradients of horizontal dispersal of cereal rust uredospores along the axis perpendicular to the wind direction across the experimental area. **5)** Uredospore dispersal gradients for the cumulative numbers of spores impacted on annuli around a 72-m-diam source.

TABLE 1. The average number of uredospores/cm² impacted during the season, 11 July through 6 August on each concentric ring of sampling stations

Ring	Radius in m	*Puccinia graminis* Spores/cm²	Fiducial limits[a]	CV[b]	*Puccinia recondita* Spores/cm²	Fiducial limits[a]	CV[b]
Center	0	53,790			14,295		
1	9	54,537	±2,075	4.55	14,954	±721	5.90
2	18	54,242	±3,092	6.38	15,350	±807	6.28
3	27	54,087	±4,354	8.08	14,129	±683	5.78
4[c]	36	34,238	±8,866	30.97	10,226	±2,022	23.56
5	72	5,421	±1,531	53.29	2,444	±320	26.90
6	108	2,154	±692	60.60	1,039	±147	26.29

[a] .05 Fiducial limits on the population mean.
[b] Coefficient of variation.
[c] Traps located at the edge of the source plot.

of wind direction and speed occurred throughout the day. Neither observations of wind conditions at 1700 hr daily nor the pattern of wind direction and movement were useful in determining the predominant downwind direction of uredospore movement. The time of day, the intensity, and the duration during which the maximum spore numbers are released is known to vary (1, 8). Presumably, the wind during the period of maximum spore liberation had the greatest effect on the pattern of spore movement.

Uredospore dispersal gradients along the downwind axis were calculated for each day, and for the cumulative numbers of both rust species. The points used for the gradients were (i) the average value of the innermost 25 stations (origin); (ii) the actual number on the downwind axis from ring 5; and (iii) the corresponding number from ring 6. When the downwind axis was one which had no station in rings 1 through 4, an average of the two adjacent stations on the same ring was used.

The rate of decrease in the log of numbers of spores/cm² impacted/m of distance from the source edge is represented by b in the regression of the form $\log \hat{Y} = a + bX$ shown in Fig. 2. Thus, the numbers of uredospores outside the source 100 m downwind of the plot decreased to about 10% of the initial spore number for both rust species. The data shown are the average cumulative number of spores that were impacted at a trap inside the source with the data for 36 and 72 m downwind being the cumulated daily totals for these downwind positions regardless of the axis on which they may have occurred.

The changes in the proportion of uredospores impacted/cm² across the entire area of the field on the axis parallel to the estimated downwind direction are shown in Fig. 3. In this graph, the calculations were based on the average value of the stations along the axis within the wheat plot as equal to 1.00 for each sampling period. The proportion of this mean was calculated for the number of spores observed at each station and plotted along this axis. The graph shows the mean of the daily proportions for the season. The spores impacted on the upwind side decreased logarithmically as the distance from the plot decreased. Inside the wheat plot, numbers of spores impacted increased 10 to 20% between the station 9 m inside the plot and the station downwind on the far side of the source plot 63 m away. Downwind from the wheat, the number of spores decreased logarithmically with distance.

Uredospore gradients perpendicular to the wind direction.—The distribution of spores on the crosswind axis for both rusts is shown in Fig. 4. This crosswind axis is perpendicular to the preceding downwind axis with the stations ordered from left to right when facing downwind. The data were converted to proportions and were plotted in Fig. 4 as was done with data plotted for the downwind axis. Again, it was necessary to use averages for the stations in rings 1 through 4 on certain days.

Considerable dispersal of uredospores occurred across the field. This movement was particularly evident in Fig. 4. Here the proportion and total number of spores trapped on the crosswind axis in rings 5 and 6 were equal to or greater than the corresponding stations of the upwind side of the downwind axis. This result could not be attributed to background spores from a source different from the wheat plot because both the upwind end and crosswind axis had more spores trapped in ring 5, 36 m from the source edge, than ring 6, 72 m from the source edge. If uredospores from a background source occurred in appreciable numbers, as many or more spores would have been trapped in ring 6 as in ring 5 at these locations. Furthermore, the number of background spores impacted at rings 5 and 6 at both ends of the crosswind axis should have been approximately equal, providing there were no major shifts in wind direction. Thus, the general relationship in which more spores were trapped in ring 5 than in ring 6 all the way around the plot indicates that most of the spores came from the central source in both the daily and cumulative counts for both rust species.

Uredospore gradients to an annulus.—The horizontal movement of uredospores to stations on annuli outside the source plot is indicated in Table 2. The net movement of spores from the plot to an annulus X distance away indicated the extent of inoculum movement around the experimental plot. In

TABLE 2. Percentage of uredospores trapped at annuli 36 and 72 m outside a source plot 72 m in diam

	Puccinia graminis		*Puccinia recondita*	
Annulus	Over source[a]	Edge of source[b]	Over source[a]	Edge of source[b]
36 m	9.99	15.83	15.17	21.94
72 m	3.97	6.29	7.02	10.16

[a] Percentage of the mean of all stations 9 m or more inside the area source.

[b] Percentage of the mean of the eight stations at the edge of the source.

general, fewer stem rust than leaf rust uredospores impacted over the whole season on traps in the annuli at 36 and 72 m from the plot. This differs from the distribution observed on the downwind axis during the same period of time, where approximately the same percentage of spores of both rusts impacted at 36 and 72 m.

Table 2 gives the percentage of the average number of spores trapped/cm^2 at annuli 36 and 72 m from the source, calculated as percentage of (i) the mean number of spores over the source; and (ii) the mean number of spores leaving the source on a horizontal plane. Deposition on the traps at these annuli was less than would be expected by loss to dilution in the horizontal plane. The circumference of the annulus at the edge of the wheat plot was 50% (3.1416 X 72) of the circumference 36 m outside the plot (3.1416 X 144) and 25% of the annulus 72 m outside the plot (3.1416 X 216). Thus, horizontal dilution alone could only account for a reduction in leaf rust from 10,226 spores/cm^2 at the plot edge to 5,114 spores/cm^2 at 36 m and to 2,557 at 72 m. The actual numbers of leaf rust spores found were 2,244 and 1,038 cm^2 at 36 and 72 m, respectively (see d_a, Table 3). Similarly, the expected reduction in stem rust spores by dilution from 34,238 cm^2 at the plot edge would be 17,119 and 8,559 spores/cm^2 at an annulus 36 and 72 m away, respectively. The numbers of stem rust spores actually observed were 5,421 and 2,154 cm^2 at 36 and 72 m, respectively (see d_a, Table 3). Thus, only 44 and 41% of the expected leaf rust spores and 32 and 25% of the expected stem rust spores were impacted at 36 and 72 m, respectively. This loss of spores in the horizontal plane presumably resulted from vertical diffusion above and below the trapping plane and loss from the system by spore deposition.

DISCUSSION.—Uredospore dispersal gradients were measured in a horizontal plane around a wheat field to determine if theoretical models of particle dispersal adequately described uredospore movement in the field. Gradients of spores or disease from a point source can be measured in three principal ways, each of which yields distinctly different slopes (6). These three different expressions of dispersal gradients were calculated for my data (Table 3) substituting the number of spores for the amount of disease and substituting the area source, a, for that of the point source, p, used by Gregory (6). Thus, d_a = average number of spores trapped (d) per unit area at various distances in all directions about an area source; D_a = summed number of spores trapped (d)

TABLE 3. Comparison of gradients in the number and percentage of *Puccinia graminis* and *P. recondita* uredospores in relation to an area source following Gregory's concepts (6)

		Stem rust		Leaf rust	
Distance from source	Ring no.	No. spores	% ring 4	No. spores	% ring 4
Mean no. uredospores trapped/cm^2 per annulus (d_a)					
0 m	4	34,237.68	100.00	10,226.20	100.00
36	5	5,421.30	15.83	2,244.17	21.94
72	6	2,153.91	6.29	1,038.56	10.16
100[a]	–	1,242.00	3.63	662.10	6.47
Calculated total no. uredospores/annulus (D_a)					
0 m	4	774,439,888	100.00	231,311,735	100.00
36	5	245,254,408	31.67	101,524,096	43.89
72	6	146,161,231	18.87	70,475,186	30.47
100[a]	–	106,130,788	13.70	56,577,451	24.46
No. uredospores trapped/unit of area downwind (d_{aw})[b]					
0 m	4	62,830.26		16,699.39	
36	5	26,132.68	48.15	6,328.10	42.78
72	6	11,220.17	20.68	2,964.35	20.04
100[a]	–	5,621.50	10.36	1,423.00	9.62

[a] Data for 100 m are extrapolated values.

[b] Percentage for d_{aw} is based on the mean number of spores trapped at a distance inside the plot at least 9 m.

per annulus of unit width at various distances around the area source; and d_{aw} = number of spores trapped (d) per unit area at various distances downwind from the area source. The differences in gradients outside the source for d_a, D_a, and d_{aw} support Gregory's concepts (6) of dispersal measurement. The gradients for d_a give the steepest slope because they include vertical and horizontal diffusion. Horizontal diffusion is accounted for in calculation of gradients for D_a by correction for the difference in circumference of the annuli. Hence, there is a flatter curve for the gradient results. The gradient for d_{aw} can be compared with Gregory's calculations for dispersal downwind (5), which indicate that 6 and 25% of the uredospores would remain airborne at 100 m if the spores were released in the open at a height of 0.1 and 1.0 m, respectively, above the ground surface. Extrapolation of my data on the downwind axis gave 10.4 and 9.6% of stem and leaf rust uredospores impacted at 100 m from the source. Thus, even with different methodology, the present data illustrate that Gregory's equations approximately describe spore dispersal for short distances in the field.

In contrast to Gregory, Schrödter (13) predicted that at least 50% of the spores of *Phytophthora infestans* will travel ca. 90 m under conditions of low turbulence and low-wind speeds. These spores have a slightly greater terminal velocity than do cereal rust uredospores. Although the present field conditions were more favorable for spore movement than those used in Schrödter's calculations, I found that less than 50% of the spores were impacted on an annulus 72 m from the edge of the source.

The regression equation can be used to predict the number of spores impacted at a distance from the source. On the downwind axis, the regression equation was of the form $\log \hat{Y} = \log a + bX$. This can be expressed in conventional terminology as $\log Qx = \log Qo + bX$, where Qx = the predicted number of spores impacted at distance X; b = the slope; and X = the distance from the source in meters. The slope from these data for b was ca. −0.0100 for both leaf and stem rust uredospores. If 10,000 leaf rust uredospores/cm² were trapped at the source, then from this formula I predict that 1,000 spores/cm² would be impacted at the same height at 100 m downwind of the source. This calculation gives approximately the same results as the data in Fig. 3.

The regression for numbers of spores impacted on an annulus was $\log \hat{Y} = \log a + b \log X$. Using the conventional terms again, then $\log Qx = \log Qo + b \log X$. The constants for the slopes are −0.4953 and −0.6002 for leaf and stem rust uredospores, respectively, from a 72-m diam source. Therefore, if an average of 10,000 stem rust uredospores were impacted/cm² at the edge of the source, I would predict that 630 spores/cm² would be impacted at an average point on an annulus 100 m away from a 72-m diam source. This equation does not enable prediction of spore movement as well as the previous one for spore movement on the downwind axis. When this prediction is compared with Fig. 5, a greater decrease with distance is indicated by the data between 36 and 72 m than predicted by the equation. However, further refinement of the equation with only three points is not justified.

Previous regression analyses have shown that the cumulative number of uredospores trapped on impaction traps was directly related to the progressive development of the rust diseases (2, 7, 10, 11). In these studies, single observations per day-replication-location-year were made. The direct comparison of location of traps at several annuli inside and outside the spore source in this study provided data for determining the effect of station location on the cumulative spore numbers. The data from all 66 stations for both rusts were analyzed for the period 11 July through 6 August. The logit transformation was used for the spore counts. The regression equation was of the form $\text{logit } \hat{Y} = a + bX$. The b values were approximately the same for all stations, but the difference between the lowest and the highest values in the innermost three rings was smaller than that between these values in the outer rings. Similarly, the differences between the highest and the lowest coefficient of determination, r^2, were less in the innermost three rings for both rust species. The result of this study confirms our earlier report (10) that stations within the plot yield data with similar values for b and r^2 to stations outside the plot. The principal difference in the stations was in the number of spores trapped. However, data from inside the plot has greater utility in disease forecasting because of the greater number of spores trapped and less variability between stations.

Results show that a spore trap located in the center of a source plot 20 m in diam should provide an adequate spore sample for analysis of the development of cereal rust epidemics. Although the data for Fig. 3 show that the number of spores impacted increase on the downwind axis across the experimental plot, 80 to 90% of the total increase from the upwind edge of the source plot occurs during the first 9 m. Thus, a large increase in the diameter of a test plot results in only a small increase in number of spores trapped.

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