

Deposition Gradients of Urediniospores of *Puccinia recondita* Near a Source

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ABSTRACT

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Deposition gradients of urediniospores of *Puccinia recondita* were measured using potted trap plants exposed at several distances between 0.1 and 3.7 m downwind of a line source of spores in the middle of a 0.4-ha, 1-m-tall crop. Trap plants were exposed for 2-3 hr on 8 days encompassing a range of average wind speeds of 2-5 m s⁻¹ measured 1.5 m above the top of the crop. After exposure in the field, the trap plants were incubated and the resulting number, *N*, of wheat rust pustules was counted. The relative

gradient of the number of pustules ($dN/dx)/N$, or $d(\ln N)/dx$, decreased with distance *x* from the source. In other words, the length scale of the deposition gradient increased with distance. These results are explained in terms of a derived equation that simultaneously accounts for the combined effects of spore deposition and dilution by atmospheric turbulence and has both an exponential and a power law component.

Additional key words: spore deposition, turbulent diffusion, wheat leaf rust.

For aerially dispersed plant pathogens, the rate of spread of disease from foci of infection depends, in large part, on the rate of decrease of the numbers of spores deposited on susceptible plants with increasing distance from the source, i.e., it depends on the spore deposition gradient. Knowledge of spore deposition gradients very near to a source is important for evaluating the effect of mixtures, or of interplanting, of susceptible and resistant cultivars of plants on the rate of buildup and ultimate severity of a disease epidemic (4,15,19). For these purposes, spore deposition gradients have often been described by empirical formulas fitted to either primary disease gradients or spore deposition gradients (12,17,19,20). These formulas are often based on measurements made at distances from one to several meters from the source and require extrapolation backwards to the source to describe inoculation of nearest neighbors and self-inoculation of the source plant.

Two equations most often used to model spore deposition gradients near ground-level sources are the power law:

$$D_p = a x^{-b} \quad (1)$$

and the exponential law:

$$D_E = A \exp(-Bx). \quad (2)$$

D_p and D_E are rates of spore deposition (spores per square centimeter per hour) at a given distance, *x*, from a source, where the subscripts *P* and *E* refer to the power and the exponential law, respectively, and exp is the base of natural logarithms. Throughout this article, distance *x* is expressed in meters so that *a* is the value of D_p at *x* = 1 m. The exponent *b* is dimensionless, *B* has units of m⁻¹, and *A* is the value of D_E at *x* = 0.

The ability of equations 1 and 2 to describe spore deposition gradients has recently been reexamined (7,8,18). Three main reasons have been advanced for preferring the use of the exponential law (Eq. 2) over the power law (Eq. 1) to describe deposition gradients. First, equation 2 predicts finite deposition at *x* = 0 and therefore can be extrapolated to zero, whereas equation 1 predicts infinite values at *x* = 0. Second, equation 2 accounts conceptually for spore deposition, whereas equation 1 does not. Third, *B*, unlike *b*, automatically carries with it explicit information about the length scale of *x*, i.e., the distance over

which the rate of deposition is reduced by a characteristic amount. Furthermore, *B* implies a constant-length scale for the deposition gradient that is considered useful for visualizing gradients (8).

The relative gradients $(dD_p/dx)/D_p$ and $(dD_E/dx)/D_E$ determined from equations 1 and 2, respectively, are:

$$(dD_p/dx)/D_p = -b x^{-1} \quad (3)$$

and

$$(dD_E/dx)/D_E = -B. \quad (4)$$

Comparison of equations 3 and 4 points up a fundamental difference between equations 1 and 2, i.e., the exponential law implies a constant-length scale (i.e., $1/B$), whereas the power law implies a length scale that increases with distance *x*.

In many instances, the length scale derived by fitting an exponential law to deposition or disease gradients depends on the range of distance over which the model is fitted, and in general, the length scale gets larger as the range of *x* of the data increases (6,7). This suggests a process whose length scale increases with *x* and is in accordance with a process dominated by turbulent diffusion. The length scale of turbulent diffusion increases with distance from a source, as larger and larger eddies come into play. Near a source of spores, both deposition and diffusion processes are simultaneously important and there simply is not one length scale that describes dispersal, as is implied by equation 2.

Near a source, the combined effects of deposition and diffusion of spores must be evaluated simultaneously. One way to do this involves solving a partial differential equation for the conservation of numbers of airborne spores per unit volume of air in and above a crop canopy (2,3,16). Unfortunately, such an equation can usually only be solved numerically, so the effects of the crop and wind parameters on spore dispersal are not readily seen.

In this paper, I present measurements of deposition gradients of urediniospores of *Puccinia recondita* near a line source of spores and compare these measurements with equations 1 and 2. I also derive a theoretical equation to help clarify the relative importance of deposition and turbulent diffusion in determining deposition gradients near a source and use this new equation to discuss under what conditions an exponential law, a power law, or neither law can be expected to describe spore deposition gradients.

MATERIALS AND METHODS

Crop and inoculum. Deposition gradients of urediniospores of *P. recondita* were measured at Mt. Carmel, CT, during June 1985

and 1986. In 1985, the studies were done in a 0.4-ha field that was planted to winter barley (*Hordeum vulgare* cv. Schuyler) in all but a 1.3-m-wide strip (seven rows) at the center of the field that was planted to winter wheat (*Triticum aestivum* cv. Ticonderoga). In 1986, dispersal was studied in the same 0.4-ha field, planted entirely to winter wheat (Ticonderoga). Both fields were planted in 0.18-m-wide, east-west-oriented rows. In both years, a central strip of wheat (seven rows in 1985 and four rows in 1986) was inoculated with urediniospores of *P. recondita* (PRTUS 6, ATCC PR 76). Inoculation in 1985 was done on 10 May and again on 29 May 1985, when the wheat was about 0.85 m tall, and inoculation in 1986 was on 20 May, when the wheat was about 0.55 m tall. This resulted in 25-m-long line sources of spores used for the spore dispersal studies. A 5-m-wide strip of crop on either side of the source, where spore trapping was done, remained free of *P. recondita* in 1985 because the barley is immune and in 1986 because a 5-m-wide strip of wheat on either side of the source rows was sprayed with triadimefon (Bayleton 50WP) on 23 May at a rate of 0.42 kg/ha. Pustules on six to 10 source plants, randomly chosen from the middle 6 m of the line source, were counted after several of the experiments to obtain an estimate for the potential strength and vertical distribution of the source of spores.

Deposition gradients. Spore deposition gradients were assessed on eight occasions by trapping spores on potted trap plants placed at various distances along a line perpendicular to and downwind of the line source. Each pot contained six to seven seedling wheat plants (cv. Ticonderoga) in the two-leaf growth stage about 10–15 cm tall.

The potted trap plants were placed at one or two heights and at several distances, between 0.1 and 3.7 m, downwind of the line source. The trap plants were positioned at a height of about 0.7 m by placing them in wire stands and at a height of about 0.2 m by setting the pots on the ground. Three replicate pots of plants, separated from each other by about 2 m along the row, were exposed at each distance and height. The area of the leaves of the trap plants was calculated from their length \times width \times 0.77. The factor 0.77 was determined from measurements of the length and width, and the area obtained with a leaf area meter, of leaves of several comparable sized potted seedling plants (D. E. Aylor, unpublished). After exposure in the field, the trap plants were kept overnight in a dew chamber and then moved to a growth chamber for 8–10 days (20 C and 12 hr light/dark; irradiance of photosynthetically active radiation of about $400 \mu\text{E m}^{-2} \text{s}^{-1}$). Three to six pots of unexposed plants from the same batch were placed among the exposed trap plants to act as controls for possible cross-contamination during incubation. When pustules developed, the number per pot was counted, and these counts were divided by the area of the plants in the pot and the length of time exposed in the field. All pustules, erupted or not, were counted. Questionable cases were verified with a $20\times$ hand lens. I assumed that numbers of pustules could be equated to numbers of effective dispersal units deposited on the plants to obtain the deposition flux of effective

TABLE 1. Dates, time, and crop conditions during the wheat leaf rust urediniospore dispersal experiments

Experiment	Date	Time ^a	Crop height ^b (m)	LAI ^c	SAI ^c
1	11 June 1985	1140–1435	1.0	2.3	2.7
2	17 June 1985	1040–1415	1.0	2.0	2.5
3	11 June 1986	1150–1505	0.9	3.0	0.9
4	16 June 1986	0920–1250	0.95	2.4	0.9
5	17 June 1986	0900–1230	1.0	2.7	1.1
6	18 June 1986	0810–1145	1.0
7	19 June 1986	1025–1325	1.0	2.2	1.1
8	20 June 1986	1310–1510	1.0

^a Local Standard Time.

^b Crop was barley for experiments 1 and 2 and wheat for experiments 3–8.

^c LAI = leaf area (one side) per ground area, or leaf area index, and SAI = projected stem area per ground area, or stem area index, for the crop.

dispersal units (*D*) (pustules per square meter per hour equal to effective dispersal units deposited per square meter per hour). In so doing, I have assumed that spores deposited at all distances from the source were equally viable and that all pustules that would develop were evident at the time of counting.

The parameters of equations 1 and 2 were estimated from linear regression analysis of log-log and log-linear transformed data, respectively. The ability of these models to fit the data was compared in the nontransformed coordinates. The residuals in the nontransformed coordinates were plotted and examined for bias.

Meteorological conditions. Wind speed was measured at heights of 0.2, 0.4, 0.8, and 1.6 m above the top of the crop canopy with sensitive-cup anemometers (C. W. Thornthwaite Associates, model 104). The height of the anemometer tower was adjusted as the crop grew. In some of the experiments, wind speed was also measured inside the canopy at a height of about 0.65 m with a hot-wire anemometer (Thermo-Systems Inc., probe model 1266). All anemometers were located 30–40 m downwind of the upwind edge of the field. Wind direction, at a height of 2.5 m, was measured with a sensitive vane (Weathermeasure Corp., model W 104). Measurements made with the vane and the hot-wire anemometer were recorded about every 4 sec, and the average and variance of these readings were calculated using a computer-controlled datalogger (CompuDAS, model 3/10).

TABLE 2. Heights of the wheat trap plants and the source pustules and the estimated number of pustules per meter length of the line sources during the wheat leaf rust urediniospore dispersal experiments

Experiment ^a	Trap height ^b (m)	Source height ^c (m)	No. pustules (m ⁻¹)
1a	0.10–0.25	0.40–0.70	75,300
1b	0.60–0.75	0.40–0.70	75,300
2a	0.10–0.25	0.50–0.70	109,600
2b	0.60–0.75	0.50–0.70	109,600
3	0.60–0.70	0.30–0.60	19,900
4	0.60–0.70	0.40–0.70	89,000
5	0.50–0.70	0.40–0.80	139,400
6	0.50–0.70	0.40–0.80	...
7	0.50–0.65	0.40–0.75	115,200
8	0.50–0.65	0.40–0.75	...

^a For experiments 1 and 2, trap plants were exposed at two heights designated a and b.

^b The range of heights indicates the extent of the trapping surface on the trap plants.

^c The range of heights indicates where 70–80% of the spore-producing pustules were located.

TABLE 3. Average meteorological conditions during the wheat leaf rust urediniospore dispersal experiments

Experiment	θ^a (°)	$u_{1.5}^b$ (m s ⁻¹)	u_*^c (m s ⁻¹)	$u \pm \text{SD}^d$ (m s ⁻¹)	RH ^e (%)	T _{air} ^e (C)	SR ^e (W m ⁻²)
1	24	2.0	0.28	0.34 \pm 0.27	35	26	700
2	56	2.5	0.37	0.24 \pm 0.18	65	23	530
3	51	2.9	0.37	...	66	27	450
4	1	2.7	0.36	0.24 \pm 0.17	89	23	330
5	51	3.6	0.46	...	50	19	800
6	67	2.5	0.32	...	55	18	570
7	32	2.4	0.30	0.34 \pm 0.24	50	24	780
8	12	4.9	0.65	...	64	21	680

^a Angle between the mean wind direction and a line perpendicular to the source.

^b Wind speed measured at about 1.5 m above the top of the crop.

^c Friction velocity (u_*) derived from the wind speed profile measured by the four cup anemometers above the crop.

^d Wind speed \pm standard deviation measured with a hot-wire anemometer inside the crop canopy at the height of about 0.65 m.

^e Relative humidity (RH), air temperature (T_{air}), and solar irradiance (SR) during the experiments.

TABLE 4. Number of pustules on wheat trap plants after exposure at various distances from a line source of *Puccinia recondita* urediniospores in the field and subsequent incubation

Distance ^a (m)	Number of pustules ^b (exp. no.) ^c									
	1a	1b	2a	2b	3	4	5	6	7	8
0.1	778	442	1,545	894	60	1,236	1,605	1,397	3,749	2,342
0.2	35	853	1,121	681	1,760	1,355
0.4	24	675	847	611	839	935
0.5	271	123	371	344
0.6	24	392	625	506	868	641
1.0	116	92	257	162	11	301	337	203	623	475
1.5	55	37	138	123
1.9	6	194	238	140	500	233
2.0	67	23	91	66
3.0	34	25
3.7	5	118	94 [†]	61	227	167
Controls	0	0	9	9	3	6	6	14	10	0

^a Distance measured from the downwind edge of the line source of infected plants.

^b Total number on 21 seedling wheat plants at each distance. A few numbers are based on counts on 18–20 plants and have been normalized to counts per 21 plants. ... = Distances not tested.

^c In experiments 1 and 2, plants were exposed at two heights (cf. Table 2).

TABLE 5. Parameters estimated by least-squares-regression fits of the exponential law [$D = A \exp(-Bx)$] and the power law [$D = ax^{-b}$] to the number of wheat leaf rust pustules per square centimeter per hour on trap plants exposed at various distances, x (m), from the downwind edge of the source

Experiment ^a	Exponential law			Power law		
	A^b	B	C.D. ^c	a^b	b	C.D.
1a	0.98	1.00	0.68	0.22	0.93	0.95
1b	0.53	0.97	0.64	0.13	0.90	0.97
2a	1.77	1.42	0.77	0.29	0.93	0.99
2b	1.20	1.29	0.90	0.24	0.82	0.94
3	0.14	0.88	0.66	0.03	0.90	0.67
4	1.36	0.60	0.68	0.50	0.63	0.87
5	1.79	0.74	0.78	0.53	0.73	0.69
6	1.29	0.83	0.67	0.32	0.84	0.75
7	3.11	0.60	0.42	1.10	0.67	0.99
8	6.29	0.64	0.59	2.11	0.70	0.94

^a The ranges of x for the data fitted were: Exp. 1, 0.1–3.0 m; Exp. 2, 0.1–2.0 m; and Exps. 3–8, 0.1–3.7 m.

^b A = number of pustules $\text{cm}^{-2} \text{hr}^{-1}$ at $x = 0$ m and a = number of pustules $\text{cm}^{-2} \text{hr}^{-1}$ at $x = 1$ m.

^c C.D. = coefficient of determination calculated in the nontransformed coordinates.

The counts of the cup anemometers were accumulated for the duration of each experiment, and an average wind speed was calculated from these counts. The variation of average wind speed with height above the crop was fitted by regression analysis to a logarithmic law, wherein the zero plane displacement height was set equal to 0.7 times the height of the crop (23). These regressions yielded values for the friction velocity u_* , which is a measure of the wind shear. Values of solar irradiance, air temperature, and relative humidity were obtained in 1985 from a standard weather station located about 200 m away and in 1986 from a weather station located near the center of the field.

RESULTS

Crop, source, and meteorological conditions. During the dispersal studies, both the barley and wheat crops were about 1 m tall and had leaf area indexes of about 2–3 (Table 1). The sources of spores were not geometrically ideal line sources in that they had horizontal and vertical extent (Table 2). The number of pustules per meter length of source, N , varied among the experiments from about 20,000 to 140,000.

Experiments were conducted under a variety of meteorological conditions (Table 3). The average wind speeds measured at about

1.5 m above the top of the crop canopy ranged from 2.0 to 4.9 m s^{-1} , whereas the friction velocity ranged from 0.28 to 0.65 m s^{-1} . Most experiments were done under conditions of moderate to strong solar irradiance and moderate relative humidity. The angle of alignment of the mean wind direction with a line perpendicular to the length of the line sources ranged from 1 to 67°. An angle of 0° corresponds to an ideal cross-wind line source.

Dispersal gradients. The number of pustules that developed on the trap plants decreased rapidly with the distance from the source (Table 4). These data were converted to deposition flux D (pustules per square centimeter per hour) and fitted to equations 1 and 2 by regression analysis (Table 5). The values of the parameters a and A (from equations 1 and 2, respectively) were generally greater for those experiments with greater numbers of pustules (Table 2) and with greater values of u_* (Table 3). These parameters are expected to increase with numbers of pustules because there are potentially more spores available for dispersal. They should increase with u_* because a larger proportion of the available urediniospores can be removed from the pustules by faster, more turbulent wind and also because spores may be more efficiently deposited at higher values of u_* . The power law was generally better than the exponential law for fitting D (Table 5). The residuals obtained when equation 1 was compared with measured D showed a relatively small amount of bias (Fig. 1A), whereas the residuals obtained by comparing equation 2 with measured D showed a marked systematic curvilinear pattern (Fig. 1B). The residuals for experiment 3 have been omitted because the counts at the two farthest distances were not appreciably above those for the controls (Table 4). The exponential law underestimated D at both ends of the range of distance over which deposition was measured. There was a trend for both b and B , but especially for B , to decrease as the range of the fitted data increased.

DISCUSSION

The deposition gradients of urediniospores of *P. recondita* measured here were described better by a power law (equation 1) than by an exponential law (equation 2). This agrees with dispersal gradients of *Erysiphe graminis* conidia measured in a wheat field by Fried et al (9) and also concurs with the findings of Roelfs and Martell (21) that the reduction in the numbers of urediniospores of *P. graminis* trapped at 30 and 60 cm from a focus could be accounted for solely by the horizontal diffusion of spores.

For a variety of crops, pathogens, and conditions, deposition gradients can often be fitted equally well by either an exponential or a power of x (6,7), particularly if the range of x is limited. The shapes of spore deposition gradients are influenced by the combined effects of loss of spores from the air by deposition and

dilution by atmospheric turbulence. The physics of this combined process, described in more detail below, suggests that gradient shapes will have both an exponential and a power law mathematical component; which component dominates the shape of the gradient depends on how rapidly a plume of spores is expanding and how rapidly spores escape from the canopy.

To better explain these concepts, I have derived an approximate equation in the Appendix which accounts for the simultaneous diffusion and deposition of spores and accounts for the case when spores are traveling entirely within the canopy as well when spores are traveling both within and above the canopy. To derive the equation, I considered an infinite ground level line source that emits spores at a constant rate and forms an expanding plume of spores downwind of the source (Fig. 2). For downwind distance $x < x_H$, the entire plume is confined within the canopy, and for $x > x_H$, some of the spores are traveling within and some are traveling above the crop height, H . The vertical growth of the plume of spores is described by either of two parameters, S_z or h , which are functions of x described in the Appendix.

The flux of spores deposited at distance x and height z , $D(x,z)$, is the product of a local deposition rate and the local aerial spore concentration. Concentration, in turn, is determined by the number of spores released per second per meter length of the line source, Q_0 , and the diffusion of spores through space. These considerations lead to the following equation for D (derived in the Appendix as equation A12):

for $x < x_H$,

$$D(x,z) = v_s Q_0 \exp[-F_1 x]/(u h), \quad (5a)$$

and for $x > x_H$,

$$D(x,z) = v_s \left\{ Q_0 \exp(-F_1 x_H) \exp[-F_2/(1-n)] \right. \\ \left. (x^{(1-n)} - x_H^{(1-n)}) \right\} / (u/h) \quad (5b)$$

The coefficients F_1 and F_2 are:

$$F_1 = v_s \text{ LAI}/(u H) \text{ and } F_2 = v_s \text{ LAI}/(u l_z),$$

where v_s is the settling speed of the spore in still air, LAI is the leaf area index of the crop, u is wind speed inside the crop canopy, and h is the height of the edge of the spore plume, which is assumed to increase with distance x according to $h = h_0 + l_z x^n$ (10,22,24). The exponent n is expected to be about 0.875 for a line source in the open (10,24), and that value will be assumed here. Equations 5a and b show that D is strongly influenced by the dilution of spores by atmospheric turbulence and looks like a power law, even inside the canopy. The main effect of deposition is embodied in the exponential term that contains the parameter F_1 . The second exponential term in equation 5b shows the reduced effect of deposition after the spore plume intersects the top of the canopy and an increasing number of spores escape the canopy (Fig. 2). The main effect of dilution is embodied in the denominator of equations 5a and b as the product of u and h .

The relative importance of deposition and dilution can be seen by evaluating equations 5a and b for values of the parameters that are reasonable for my experiments (Fig. 3). Because urediniospores are forcibly removed from pustules by wind, I have assumed that u inside the canopy is reasonably given by u_c (25). In Figure 3, all values have been normalized to equal unity at $x = 0.1$ m. For this example, the relative change in the number of spores in the air, $Q(x)$, is much less than it is for turbulent transport and dilution, $T(x)$, and thus has little effect on the value of $D(x,z)$. This agrees with the behavior of D for the urediniospores of *P. recondita* measured here, which gave essentially straight lines in $\log(D)$ vs. $\log(x)$ coordinates over a range of 0.1–3.7 m.

Deposition should have a stronger effect on the total deposition integrated over the entire depth of the canopy, D_T , than it does on D . Although I did not measure D_T , I calculated it using equation A7 of the Appendix and have plotted it in Figure 3 for comparison with D . For $x < x_H$, D_T is determined solely by spore deposition

and is described by an exponential law. As soon as spores start to escape from the canopy, however, dilution begins to dominate dispersal and D_T also is described better by a power law than by an exponential law.

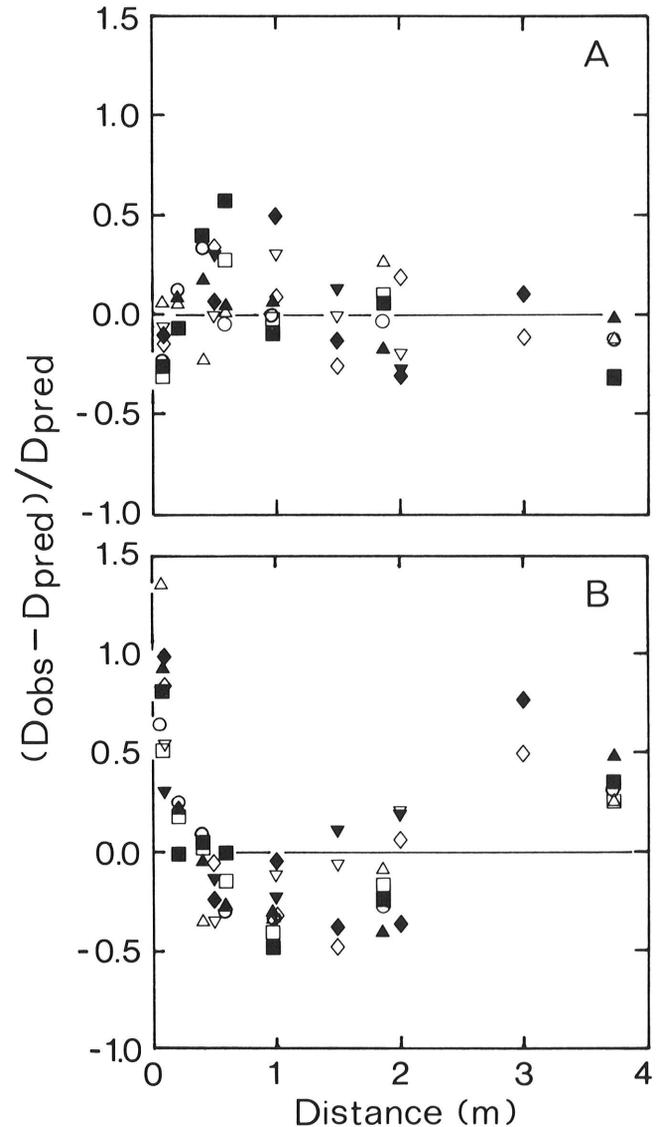


Fig. 1. Residuals $[(D_{\text{observed}} - D_{\text{predicted}})/D_{\text{predicted}}]$ in the nontransformed coordinates for the number of wheat leaf rust pustules on trap plants vs. distance from the source of spores for experiments 1a, 1b, 2a, 2b, 4–8 (unfilled and filled diamonds, unfilled and filled inverted triangles, circles, unfilled and filled squares, unfilled and filled upright triangles, respectively), where the predicted values were A, by the power law (Eq. 1) and B, by the exponential law (Eq. 2).

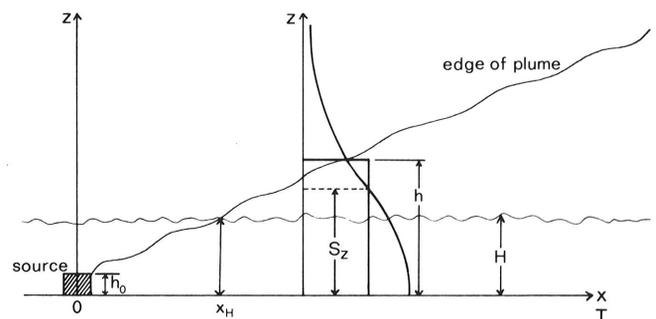


Fig. 2. Schematic plan view of a plume of spores expanding downwind from a line source of spores.

Ideally, a model should describe spore deposition gradients well over a large range of distances. Accurate estimates of deposition very near a source are required to calculate the buildup of disease around a focus, whereas accurate estimates at distance are required because diseases often spread in a series of discrete jumps away from the disease front (18). The length scale of the spore dispersal process changes with distance from a source and the exponential law, with a constant B , generally cannot simultaneously describe spore deposition gradients both near to and far from a source, and it will usually underestimate D at both extremes of distance.

McCartney and Bainbridge (17) found that deposition gradients for droplets released inside a barley canopy were described about as well by either equation 1 or 2. The success of the exponential law in fitting their data was probably not because deposition dominated dispersal, however. Deposition was apparently of minor importance in determining gradients in their experiments, just as it was in the present experiments. One way this can be seen is by comparing the values of B estimated from regression analysis with estimates of the parameter F_1 of equations 5a and b. To estimate the importance of deposition in McCartney and Bainbridge's study, I used data from their Table 4 to obtain B and their Table 7 to obtain an equivalent F_1 . Excluding their experiment 8, for which the wind speed was very low (0.05 m s^{-1}), the mean value of B/F_1 was about 8 (range 6.2–12.4). The present study yielded a mean value for B/F_1 of 7.4 (range 4.4–14.4). In other words, in both studies, deposition could directly account for only about one-eighth of the reduction in deposition with distance, and the major factor causing the reduction was turbulent diffusion.

When fitting an exponential law to deposition data, the value of B often depends on the range of x over which the data are fitted and tends to decrease as the range of x increases. The values of B found by McCartney and Bainbridge (17) ranged from about 1.4 to 2.8 m^{-1} , whereas in my experiments, B was generally between 0.6 and 1.0 m^{-1} . These differences are probably mainly a reflection of the difference in the range of x used in the two experiments. McCartney and Bainbridge measured deposition over 0.15–1.5 m. The range of x was 0.1–3.7 m for my experiments 3–8, which gave the lowest values of B (Table 5). In my experiment 2, where the range of x was 0.1–2.0 m, the value of B was closer to those found by McCartney and Bainbridge.

Equations 5a and b suggest that loss of spores from the air by deposition will determine the shape of the deposition gradient,

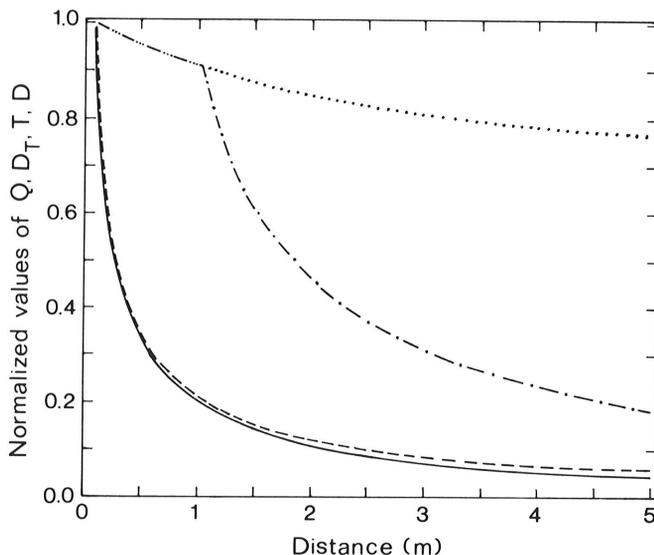


Fig. 3. Relative variation with distance from the source plotted for: number of airborne spores, Q (dotted line); total deposition flux summed over all heights in the canopy, D_T (dot-dashed line); transport and dilution function, T (dashed line); and deposition flux for a particular height in the canopy, D (solid line). These quantities were calculated by the model derived in the Appendix for $v_s = 0.01 \text{ m s}^{-1}$, $u = 0.3 \text{ m s}^{-1}$, $h_0 = 0.1 \text{ m}$, $l_2 = 1$, $n = 0.875$, and $\text{LAI} = 3$.

measured at a particular height, z , only when wind speed in the canopy, u (or u_s), is low and when turbulent diffusion is slight. For spores such as urediniospores of the rusts, which become airborne mainly when the wind is gusty, it seems that diffusion could dominate dispersal much of the time and gradients would be modeled better by a power law than by an exponential law. On the other hand, for spores such as sporangia of the downy mildews, which can be released independently of wind speed, it is likely that deposition will sometimes dominate dispersal, and gradients will sometimes be modeled better by an exponential law than by a power law.

The power law as written in equation 1 is said to have the difficulty of predicting infinite concentrations at the source. The problem arises in assuming that a source is located at the mathematical point zero. Real sources of spores have finite size, of course, and there is a maximum concentration of spores possible, obtained by dividing the number of spores at the source by the finite volume of the source. As an extreme example, consider the concentration of urediniospores within a single bean rust pustule incited by *Uromyces phaseoli*. Reasonable values for the number of urediniospores per pustule and the volume of a pustule are 1,000 urediniospores and 0.01 cm^3 , respectively (14). For these values, the absolute maximum initial concentration C_0 at the source, with the spores still resting on the leaf, is 10^5 spores per cubic centimeter, clearly a finite number. During the removal process, spores are likely to be mixed, more or less instantaneously, throughout a volume, V_0 . The size of V_0 probably depends on the gustiness of the wind, the size of leaves of the host, the density of leaf area in the canopy, and the vertical location of the source within the canopy. The volume V_0 is likely to be at least L^3 (m^3), where L is the width of the leaf, and may be as large as H^3 (m^3), where H is the height of the crop. Thus, for a single bean rust pustule on a 10-cm-wide bean leaf in a 0.5-m-tall crop, a more realistic estimate of C_0 in the air at the source, assuming that all of the spores contained in the pustule are released at once, is between 10^2 to less than one spore per cubic centimeter depending on whether V_0 is determined by L or H .

Equation 1 can be modified to avoid the problem of infinite concentrations at $x=0$ by adding a constant to x before raising it to the power b as was done by Mundt and Leonard (19). This amounts to translating the y -axis c units to the left. They obtained:

$$y + a(c+x)^{-b} \quad (6)$$

where the parameters a , b , and c were fitted simultaneously by nonlinear regression analysis. In air-pollution modeling, the effect of a finite-sized source of material is sometimes accounted for by assuming that material is emitted from a virtual point source located at a distance x_c upwind of the source. This leads to (24):

$$y = c_0 + a(x + x_c)^{-b} \quad (7)$$

The parameter c_0 is related to the initial size of the source and the distance x_c depends both on the size of the source and on atmospheric stability through its effect on turbulent diffusion. My equations 5a and b contain a parameter, h_0 , which is intended to account for the size of the source in the same spirit as the c_0 of equation 7. From equations 5, I expect that a finite h_0 would tend to cause some initial downward curvature of lines of $\log(D)$ vs. $\log(x)$. My data fell essentially on a straight line with no discernible curvature and, therefore, I was unable to estimate h_0 .

The problem of estimating self-inoculation of a host leaf or plant is, unfortunately, still unresolved. An exponential fit to data and extrapolated backwards to the source will generally underestimate deposition near the source and, furthermore, the estimate will depend on the range of x for the data that was fitted. An exponential law could probably give good estimates if its parameters were derived entirely from total integrated deposition data, i.e., D_T , measured within the short distance from the source before spores start to escape from the canopy. However, this distance may often be too short to allow sufficient measurements. On the other hand, the estimate made from a

modified power law, such as equation 6, depends greatly on the parameter c . Although c is probably related to source size, it is still extremely difficult to estimate its value from first principles. Finally, if transfer of spores on the same plant or between neighboring plants occurs by leaves touching one another, then it may not be possible to estimate this transfer of spores by extrapolating any equation that has been fitted to deposition data, even though it may have been measured entirely within the range of validity of the exponential law.

APPENDIX

The equations for describing spore deposition gradients developed here are based on an adaptation of Chamberlain's so-called source depletion model (5,11). They will be derived for an infinite line source, which emits spores at a constant rate, and is conceived of forming a plume of spores downwind of the source (Fig. 2). In this case, the concentration, C (no. m^{-3}), of spores in the air is given by (1,5,13):

$$C(x,z) = Q(x) T(x,z), \quad (A1)$$

where Q (no. $s^{-1} m^{-1}$) is the number of spores released by the source that are still airborne (i.e., have not yet been deposited) at some downwind distance x , and T ($s m^{-2}$) is the transport function, which describes the dilution of the plume of spores by atmospheric turbulence.

Often, as was the case in my experiments, deposition is measured along a line at a particular height, or range of heights, in a crop canopy. This measures the rate of deposition of spores D (spores per square meter per second) at a particular measurement height, z , which is equal to:

$$D(x,z) = v_d C(x,z), \quad (A2)$$

where v_d is a spore deposition velocity. The total deposition on the entire depth of the crop canopy per unit ground area, D_T (no. $s^{-1} m^{-2}$), is obtained by first multiplying equation A2 by the leaf area density, LAI/H , where LAI is the leaf area of the crop per unit ground area and H is the height of the crop canopy, and then integrating this over z , which gives:

$$D_T(x) = \int_0^z (v_d LAI/H) C(x,z') dz'. \quad (A3)$$

The limits of integration over z in equation A3 are from 0 to h for $x < x_H$ and from 0 to H for $x \geq x_H$, where h is a measure of the vertical spread of the plume of spores, defined below, and where x_H is the distance from the source at which the plume edge intersects the top of the canopy (Fig 2).

For a line source at ground level, T is a function of the vertical direction, z , given by (1,10,22):

$$T(x,z) = 1/[(2\pi)^{0.5} u S_z] \exp(-z^2/2 S_z^2), \quad (A4)$$

where u is the average horizontal wind speed at source height and S_z is a diffusion parameter that is a function of x and measures the vertical spread of the plume of spores. I will simplify greatly here by ignoring this complicated dependence of T on z and assume a "top hat" distribution for T . Thus, I use h , instead of S_z , as the measure of the vertical spread of the plume.

Near the source, the vertical extent of the spore plume, h , is taken to vary as (10,22,24):

$$h(x) = h_0 + l_z x^n, \quad (A5)$$

where l_z is a constant-length scale parameter and where the power n is expected to be about 0.875 for a line source. The constant h_0 is the initial vertical extent of the spore plume and assures finite values of C as x approaches zero (18). The value of h_0 depends on the vertical distribution of pustules in the canopy and on the turbulent intensity of the wind; h_0 is extremely difficult to specify

but it is probably about one-quarter of the vertical extent of the source (24).

Thus, instead of using equation A4, I assume T can be described by:

$$T(x) = 1/[u h]. \quad (A6)$$

This simplified transport function is consistent with Chamberlain's source depletion model, which assumes that spores are removed uniformly from throughout the depth of the spore plume. I also assume that leaf area is distributed uniformly in height and that $v_d = v_s$, where v_s is the settling speed of the spore in still air (1,5). These assumptions greatly simplify the estimation of deposition in the crop, so that the integral in equation A3 can be replaced by the expression obtained below.

The number of spores in the air decreases with increasing distance from the source because spores are lost by deposition, so that:

$$D_T = -dQ(x)/dx = R(x) Q(x), \quad (A7)$$

where the second equality results from the integration of equation A3, and I have assumed that v_d and LAI/H are constant with height in the canopy. R (m^{-1}) is an effective average probability of a spore being captured per unit distance, or in other words, R is a product of an efficiency of capture, E , and the average leaf area density, (LAI/H) . Here, I have assumed that E is approximately v_s/u (13). From equation A3, $R(x)$ becomes:

$$R(x) = (v_s LAI)/(u H) \text{ for } x \leq x_H \quad (A8a)$$

$$R(x) = (v_s LAI)/(u h) \text{ for } x > x_H \quad (A8b)$$

For simplicity, I have ignored deposition on the ground, but this could be accounted for approximately by replacing LAI by $(1 + LAI)$.

Integrating equation A7 leads to:

$$Q(x) = Q_0 \exp \left\{ - \int_0^x R(x') dx' \right\}. \quad (A9)$$

As long as most of the spores are inside the canopy, i.e., for $x \leq x_H$, Q is simply:

$$Q(x) = Q_0 \exp \left\{ -[(v_s LAI)/(u H)] x \right\}. \quad (A10)$$

On the other hand, for $x > x_H$, Q becomes:

$$Q(x) = Q(x_H) \exp \left\{ -(v_s LAI/u) \int_{x_H}^x h^{-1} dx \right\} \quad (A11)$$

where $Q(x_H)$ is the number of spores airborne at $x = x_H$.

Although it is difficult to integrate equation A11 (after substituting equation A5) analytically for arbitrary n , it can be integrated if h_0 is assumed to be negligible compared with $l_z x_H^n$, which seems reasonable for $x > x_H$ for a small enough source. Finally, I obtain D by carrying out this integration and combining the results with equations A1 and A2. For $x < x_H$, I obtain:

$$D(x,z) = v_s Q_0 \exp[-F_1 x]/(u h), \quad (A12a)$$

and for $x > x_H$, I obtain:

$$D(x,z) = v_s \left\{ Q_0 \exp(-F_1 x_H) \exp[-F_2/(1-n)] (x^{(1-n)} - x_H^{(1-n)}) \right\} / (u h). \quad (A12b)$$

The coefficients F_1 and F_2 have been written to simplify the equations and are:

$$\begin{aligned} F_1 &= v_s LAI/(u H) \\ F_2 &= v_s LAI/(u l_z). \end{aligned} \quad (A13)$$

Equations A12a and b show that deposition at a particular height in the canopy, D , is given in the form of a product of an exponential and a power law. Thus, D could vary more according to either an exponential law or a power law, depending on the values of the parameters F_1 , F_2 , and h_0 . This formulation is applicable for experiments where deposition gradients are determined from lesions on a leaf at a fixed height in the canopy, or from pustules on trap plants exposed at a fixed narrow range of heights in the canopy, as in the present study. For examining an epidemic, the total deposition over the entire depth of the canopy, D_T , is of interest. To obtain D_T requires that lesions be counted on all of the leaves on an entire plant. Although D_T is seldom measured, it can be calculated by combining equations A7, A8, A10, and A11. As long as the entire spore plume remains in the crop ($x \leq x_H$, Fig. 2), D_T should follow an exponential law. As soon as spores start to escape from the canopy ($x \geq x_H$, Fig. 2), however, dilution starts to affect D_T , the length scale of dispersal is no longer constant, and the exponential law starts to give way to the power law. Depending on the vertical location of the source in the canopy and the intensity of turbulence in the atmosphere, x_H can be located very close to the source so that an exponential behavior for D_T may only hold for a very short distance from the source and may not be discernible in observed gradients.

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