

Initial Spread of Bean Rust Close to an Inoculated Bean Leaf

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ABSTRACT

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Foci of bean rust were established in a bean field by inoculating single trifoliolate leaves with urediniospores of *Uromyces appendiculatus*. The initial spread of disease from these foci was quantified by counting the number of pustules on entire plants within 3 m of the inoculated plant. A model was derived for spore deposition close to a source based on the assumption that spores move in approximately straight line trajectories within a few meters of a source. This model leads to an equation of

the form $P_1 = A(1 + s^2/L^2)^{-1}$, in which P_1 is the number of pustules per leaf on individual plants, A and L are parameters of the model, and s is distance from the source. The observed primary spread of bean rust was described well by the model, with the parameter L determined from the size of the plants. The scaling parameter A is related to the number of spores released at the source and is the only adjustable parameter in the model.

Additional keywords: autoinfection, spore dispersal, quantitative epidemiology

The spatial and temporal development of a plant disease epidemic depends strongly on the spatial distribution for dispersal of pathogen inoculum (6,21,22). Of particular importance is the relative number of the spores produced on a plant that re-infect the same plant (autoinfection) compared to the number that infect other plants in the field (alloinfection) (25). The ratio of autoinfection to the amount of infection on distant plants is also im-

portant for predicting the potential efficacy of crop mixtures for reducing disease (2,17,18,23-26) and for estimating the potential loss in crop yield due to disease spread from foci (9,10). To model this spatial apportionment of inoculum requires a mathematical description of spore deposition that is valid over a wide range of distances from a source.

Rust diseases, such as those caused by *Puccinia* spp. and *Uromyces appendiculatus* (Pers.) Unger, are spread by airborne spores. For these organisms, spore deposition and the amount of disease due to primary infection decreases rapidly with distance

number of leaves on the plant. This allowed us to maintain a plant as the sampling unit and helped to reduce variation due to size differences among plants. Linear regressions of $\ln(P_i)$ versus $\ln(s)$ were carried out separately for the east and west half of the source rows. No significant differences were found in the regression coefficient of $\ln(s)$, which corresponds to the exponent of distance in a power law. Thus, we assumed spore deposition to be a separable function of distance and angle, and the data from the various angles were pooled.

MODEL OF SPORE DEPOSITION CLOSE TO A SOURCE

As Gregory (14) pointed out, the decrease of spore deposition with increasing distance from a source is determined by the geometry of the source and related to the dimensions of the space (i.e., one, two, or three) into which spores are dispersed. From geometrical considerations alone, in the absence of deposition (or for weak deposition), one can conclude that aerial spore concentration (and consequently spore deposition) should decrease

TABLE 1. List of symbols

Symbol	Explanation [units] ^a
a	Scaling parameter for power law model equation [m^{-b-2}]
a_p	Leaf area of a plant [m^2]
A	Scaling parameter which relates the number of spores released at the source to the number of resulting infections on surrounding plants []
b	Exponent of the power law equation []
B	Rate of spore deposition per unit pathlength through the canopy [m^{-1}]
c	Length scale used to shift origin in the modified power law equation (23) [m]
C	Aerial spore concentration [m^{-3}]
d	Extent of a plant in the x direction [m]
D	Rate of spore deposition per plant at distance s from the source [s^{-1}]
D_0	Rate of spore deposition to the source plant [s^{-1}]
F	Unit vector in the direction of a spore trajectory []
g	Parameter related to the rate of spores released at the source [s^{-1}]
H	Height of the crop canopy, or height of a plant [m]
L	Length scale, characteristic of the size of a plant [m]
LAI	Leaf area index []
m	Constant which accounts for the enhanced deposition to the source plant due to reflection of spores from the ground []
N_i	Number of leaves per plant []
P_i	Initial number of pustules on inoculated leaves []
P_l	Number of pustules per leaf on individual plants []
P_p	Number of pustules per plant []
Q	Rate of release of spores at the source [s^{-1}]
r	Radial distance $\{=\sqrt{(x^2 + y^2 + z^2)}\}$ from the source [m]
r_1	Correlation coefficient []
R	Radius of a hypothetical spherical plant [m]
s	Horizontal distance $\{=\sqrt{(x^2 + y^2)}\}$ between the source and receptor plants [m]
s'	Length of the specularly reflected (from the ground) trajectory between the source and receptor plants [m]
T	Air temperature [$^{\circ}C$]
u	Mean horizontal speed of spores in the canopy [$m s^{-1}$]
u_r	Outward radial component of spore velocity [$m s^{-1}$]
v_s	Settling speed of a spore under gravity [$m s^{-1}$]
V	Volume of a plant [m^3]
W	Width of a plant [m]
$d\omega$	An element of solid angle through a plant []
x, y, z	Coordinates of a Cartesian coordinate system in the downwind, crosswind, and vertical directions, respectively []
Y	Number of spores deposited, or number of infections, per unit area [m^{-2}]
θ, Φ	Angles defining the direction of a simulated spore trajectory (Fig. 2) []

^a Dimensionless quantities are indicated by open square brackets [] following the explanation.

with distance from a source according to a power law, excluding a relatively small region close to a source (1). In fact, both spore deposition and primary disease gradients for many diseases including the rusts of bean, wheat, oat, and corn do decrease according to an inverse power of distance from the source (1,6,12,23). Here we derive a model for spore deposition close to a source which accounts for the geometry of the plant. Symbols are explained in Table 1, and physical dimensions of the quantities are specified within square brackets.

For a broad-leaved plant canopy, deposition of spores occurs mainly by sedimentation (19). In this case, the rate of deposit per unit of pathlength through the canopy, B (m^{-1}), is approximately equal to (1):

$$B = v_s LAI / (uH), \quad (1)$$

where v_s is the settling speed of a spore under gravity, LAI is the leaf area index, u is the horizontal speed of airborne spores in the canopy, and H is the height of the canopy. For urediniospores of *U. appendiculatus*, $v_s = 1.2 \text{ cm s}^{-1}$ (11). In the present study, during spore release H increased from about 0.2 m to 0.3 m while LAI increased from 0.7 to 1.1 (see Results). For the wind conditions of the present experiments (Table 2), we can expect the mean wind speed within a bean canopy of these dimensions to range between 0.2 m s^{-1} and 0.6 m s^{-1} (Aylor, unpublished). Therefore, B should range between 0.08 and 0.20 m^{-1} . In other words, the length scale for deposit in the exponential term (1) (i.e., B^{-1}) is between 5 and 12 m, which is much larger than the width of a bean plant (0.15–0.5 m). Spore release occurring during gusts of wind would tend to further increase these length scales (3–5).

The rate of spore deposition, D (s^{-1}), to an entire plant which has leaf area a_p and occupies a volume V is given by (1):

$$D = \iiint_V \{v_s a_p / V\} C dV, \quad (2)$$

where C is the aerial spore concentration. Since we are interested in describing deposition on the source plant itself and on its immediate neighbors, we will focus our attention on deposition

TABLE 2. Meteorological conditions during the dispersal of urediniospores of *Uromyces appendiculatus* resulting in the observed initial spread of bean rust from inoculated leaves

Days after planting ^a	T_{day}^b ($^{\circ}C$)	T_{wet}^c ($^{\circ}C$)	Wetness duration (hr)	Wind speed ^d (m/s)	Wind direction ^d ($^{\circ}$)	Rain (mm)
26	21.7	18.9	15.0	2.8	185	...
27	19.4	18.7	12.6	1.5	95	...
28	19.7	18.0	7.1	2.0	21	2.5
29	21.7	21.7	11.9	2.3	175	...
30	25.0	21.6	8.3	2.8	354	...
31	24.3	19.1	11.5	1.6	29	...
32	25.1	22.9	9.5	2.3	184	...
33	26.8	22.8	10.9	2.1	300	5.3
34	26.5	22.8	5.0	3.0	188	...
35	23.6	15.7	1.8	2.8	303	5.6
36	19.9	15.7	9.0	2.7	330	...
37	19.3	17.3	11.2	2.1	214	...
38	20.2	18.4	6.4	1.8	117	...
39	20.8	16.4	11.6	2.8	83	...
40	22.1	20.5	7.0	2.2	228	...
41	24.1	20.8	11.2	2.4	315	...
42	26.1	25.0	1.0	3.2	183	...
43	26.9	23.6	10.9	2.1	267	...
44	26.6	22.5	9.4	3.8	196	...
45	21.2	20.2	9.7	3.0	341	13.7
46	17.3	13.0	6.2	3.0	311	...

^a Planting was on 23 June.

^b Average air temperature for the day 0000–2400 hr.

^c Average air temperature during the hr of moisture duration, i.e., during the night of the day indicated and the early a.m. of the next day.

^d Average wind speed and direction during the period 0800–2000 hr.

on plants within distances of less than 2–3 m from a source. Urediniospores of rusts become airborne mainly during gusts of wind (1). Thus, over such short distances it seems reasonable to assume that spores will travel outward away from a source in approximately straight lines (20). If we neglect the relatively small amount of depletion of airborne spores due to deposition, then C at a radial distance $r = \sqrt{(x^2 + y^2 + z^2)}$ from a source of spores of strength $Q(s^{-1})$ located at the origin is:

$$C = Q/(u_r 4\pi r^2), \quad (3)$$

where u_r is the outward radial velocity of spores. Substituting this expression into equation 2 we obtain:

$$D = \iiint_V \{v_s a_p / V\} [Q/(u_r 4\pi r^2)] r^2 dw dr, \quad (4)$$

where $dV = r^2 dw dr$ and where $dw = \sin \theta d\theta d\phi$ is an element of solid angle (29) through a plant. If we assume that the source plant is a sphere of radius R with its center at the source of spores, then equation 4 yields:

$$D_0 = QRv_s a_p / (u_r V). \quad (5)$$

This expression neglects the possibility of reflection of spores

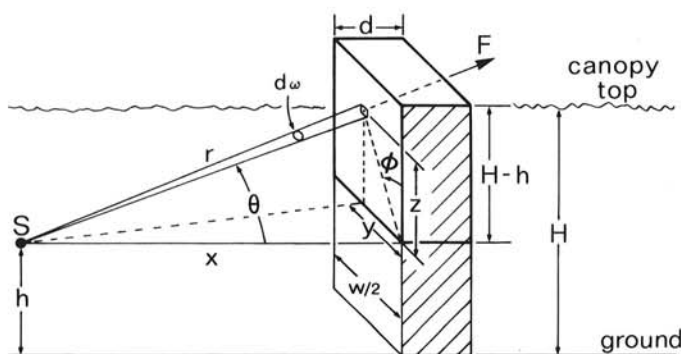


Fig. 2. Schematic drawing defining the geometrical terms used in the numerical simulation spore deposition model.

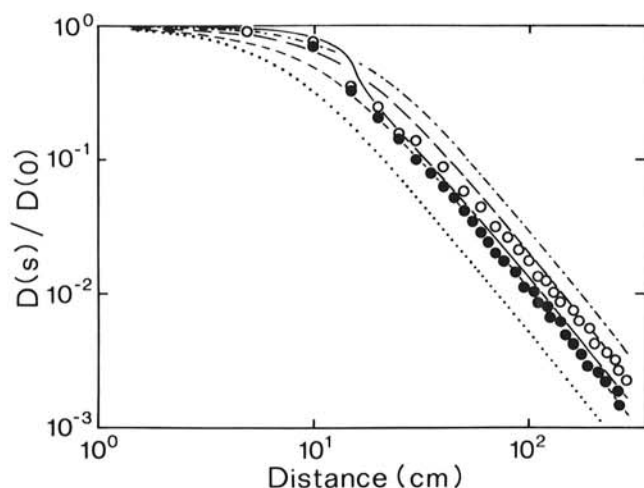


Fig. 3. Relative deposit per plant calculated for a spherical plant using equation 6 with $R = 14.9$ cm (solid line) and for a parallelepiped (Fig. 2) with $W = 33$ cm, $H = 21$ cm, and $d = 20$ cm using the simulation model for $h = 1/2 H$ and $h = 2/3 H$ (solid dots) and for $h = H$ (open circles). The four broken lines were calculated using equation 8a with L^2 (cm^2) = 50 (dotted), 100 (short dashed), 200 (long dashed), and 300 (dot-dashed).

from the ground, and only accounts for deposit due to the first pass of spores through the plant. A portion of the spores are reflected from the ground. This effectively increases the pathlength through the plant and enhances deposition. We will account for this reflection below. The fact that a power law predicts infinite concentrations at the origin presents no problem in evaluating equation 4 because the spherical symmetry yields a volume element proportional to r^2 which removes the singularity at the origin.

The deposit on any plant can be obtained from equation 4 once the triple integral is evaluated over the volume occupied by the plant. For an arbitrarily shaped plant close to a source, this triple integral is very difficult to evaluate in closed form except for a hypothetical spherical plant. For a spherical plant of radius R with its center at source height ($z = R$), and assuming that spores are reflected from the ground without loss, we obtain:

$$D = D_0 \{1 - (s^2 - R^2)/(8sR) \cdot \ln[(s+R)^2/(s-R)^2] - (s'^2 - R^2)/(8s'R) \cdot \ln[(s'+R)^2/(s'-R)^2]\}, \quad (6)$$

where D_0 is the rate of deposit to the source plant from non-reflected spores (given by equation 5). Here, $s = \sqrt{(x^2 + y^2)}$ is the horizontal distance from the source to the center of a plant at distance s , and $s' = 2\sqrt{(R^2 + (s/2)^2)}$ is the length of the specularly reflected trajectory that extends from the center of the source plant to a point on the ground halfway to the plant of interest and then from there to the center of this plant. This trajectory is the path of spores "reflected" from the ground (8). In deriving equation 6, we have assumed total reflection of spores from the ground. That is, we have neglected the relatively small deposit of spores on the ground, within 1–3 m from the source, expected for bean rust spores entrained from pustules by turbulent wind (5,12). Note that care must be taken in evaluating equation 6 around the apparent singularities at $s = 0$ and $s = R$. However, at both of these points, the limit of the function is well behaved and is: $D(s = 0) = 1.09D_0$ and $D(s = R) = 0.57D_0$.

We evaluated the effect of a more realistic plant shape (i.e., the parallelepiped shown in Fig. 2) using a numerical Monte Carlo simulation. In the simulation, plants were represented as rectangular parallelepipeds with dimensions d , W , and H in the x , y , and z directions, respectively (Fig. 2). The source was located at the point $(x, y, z) = (0, 0, h)$. A spore was assumed to move radially outwards along the direction of the unit vector F , located by colatitude angle θ and azimuthal angle ϕ . For each spore trajectory, θ and ϕ were randomly chosen from a uniform distribution over the total solid angle. Trajectories which intercepted the ground plane ($z = 0$) were specularly reflected upwards.

The leaf area density was assumed to be uniform over space, and the outward radial spore velocity was assumed to be constant. Thus, the probability for a simulated spore to deposit on foliage was taken to be proportional to the length of its trajectory within a model plant. For each simulation, we calculated 20,000 spore trajectories and determined the length of each trajectory passing through a model plant located at distance x from the source. This accounting was done for a series of plants located at various distances. The total length of all trajectories passing through each model plant was obtained by summing the individual lengths. Finally, the relative amount of deposit on each plant was determined by dividing each sum by the result obtained for the model plant centered at the origin.

Although this numerical solution gives the desired result, we would prefer a simpler equation (even an approximate one) which would be easier to fit to data. At relatively large distances from a source, C remains relatively constant over the extent of a single plant. Equations 2 and 6 evaluated at $s = 0$ and in the limit as $s \rightarrow \infty$, yield:

$$D(s = 0) = mD_0 \quad (7a)$$

$$D(s \rightarrow \infty) = (2/3) D_0 R^2 / s^2 = 2 v_s a_p Q / (u_r 4\pi s^2), \quad (7b)$$

where D_0 is given by equation 5. The factor m ($m = 1.09$ for a spherical plant) in equation 7a and the factor 2 in equation

7b account for the additional deposit of spores on plants due to their reflection from the ground (8). At large distances from the source, the deposition is independent of the shape of the plant because there is negligible divergence of spore concentration for trajectories traversing the plant.

We propose a simple equation for the rate of spore deposition per plant at distance s , i.e., $D(s)$, which has the proper physical behavior for both small and large values of s , i.e.:

$$D = g(1 + s^2/L^2)^{-1}, \quad (8a)$$

for which:

$$D(s=0) = g \quad (8b)$$

$$D(s \rightarrow \infty) = gL^2/s^2. \quad (8c)$$

Here, g is a parameter related to the strength of the source of spores and L is a length scale characteristic of the extent of a plant. This result is similar in form to equations derived elsewhere (1,9).

To evaluate L , we must eliminate the scaling factor g from the above equations. We do this by dividing the asymptotic value (equation 8c) by the value at the origin (equation 8b). We arrive at the desired expression for the parameter L by setting this ratio of $D(s \rightarrow \infty)/D_0(s=0)$ equal to the equivalent ratio given by equations 7a and 7b. This yields:

$$L^2 = (2/3m)R^2 = V/(2\pi mR). \quad (9)$$

Equation 9 was derived for a hypothetical spherical plant for which $m = 1.09$. The results of the numerical simulation model (Fig. 3) showed that an analogous equation holds for a plant in the shape of a rectangular parallelepiped, as long as R is an equivalent radius given by the geometric mean of the half-lengths of the three sides. The reflection parameter m was also found to be approximately equal to 1.09 for a parallelepiped-shaped plant with the dimensions of our bean plants (see Results).

Finally, we assume that the number of pustules on a plant is directly proportional to the rate of spore deposit given by equation 8. Then, replacing g by AN_1 , where we have introduced N_1 to help account for variation in the size of plants, we obtain:

$$P_p = AN_1(1 + s^2/L^2)^{-1}. \quad (10)$$

We used the value of L^2 given by equation 9 and determined a value of A for each source using regression analysis. To help account for the increased variance in counts with increasing counts, we transformed equation 10 by taking the square root of both sides (28), before carrying out the regression analysis.

RESULTS

Development of the crop. The plants emerged 8–9 days after planting, and the first pods were of prime harvest size on day 48, when the final counts of pustules were made. Increases in plant height and leaf area were rapid during both periods of disease spread (Fig. 4). The average number of plants per meter of row was about 12.8, yielding an LAI for the crop of about $0.167 \times$ leaf area per plant (dm^2), or about 0.8 on day 30 and about 1.6 on day 40. Plants had an average of 7.1 and 8.8 trifoliolate leaves when the first and second set of pustule counts were made, respectively. On day 48, average (\pm SD) plant height, width within the row, and width across the row (in centimeters) were: 45.6 ± 2.9 , 33.6 ± 7.2 , and 56.9 ± 7.5 , respectively. On the average at this time, the foliage of one plant overlapped to some extent with that of four other neighboring plants within the same row.

Weather. Conditions were generally favorable for infection and disease development during the experimental periods (15,16) (Table 2). There was relatively little difference in either the direction or the speed of the wind during the two periods of primary

disease spread (Fig. 5), which were arrived at from observations of the times pustules were open on inoculated and uninoculated leaves and an estimate of the latent period of the pathogen. During both periods, wind direction was most frequently perpendicular to the rows. There was a tendency for the highest wind speeds to be associated with winds from the northwest, and there were very few occasions of wind from the east. There were two occasions of light rain during the periods of spore dispersal.

Results of model calculations. The three methods of calculating D (i.e., equation 6, equation 8a, and the numerical simulation) all gave similar results (Fig. 3). All methods demonstrated a relatively flat "shelf" region (on a log-log plot) for distances from the origin of less than about 10–15 cm, and all approached slopes of -2 for distances > 15 cm. The results of the numerical simulation for a parallelepiped-shaped plant and the closed form solution for a spherical plant are in generally close agreement. The four curves given by equation 8a demonstrate the sensitivity of this model to the parameter L . The predictions of equation 8a with values of L^2 between 100 and 200 cm^2 essentially bracket the results of equation 6 and the simulation model. The relatively steep decrease in deposit that is predicted by equation 6 around $s = 15$ cm and is predicted by the numerical simulation around $s = 10$ cm occurs when a plant first envelops the point source. This is an artifact of the sharp boundaries we have placed on the spatial extent of the model plants. For more realistic leaf density distributions which taper off gradually at the edges of

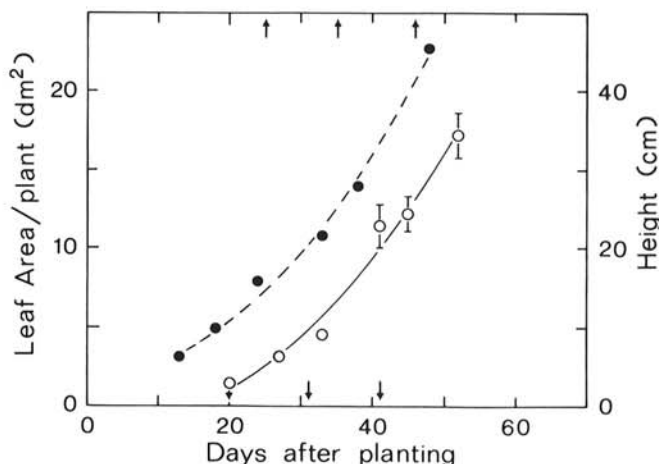


Fig. 4. Increase with time after planting of the average leaf area per plant (open circles) and average plant height (filled circles) in the bean crop. Two sets of three arrows, along each of the lower and upper horizontal axes, indicate (from left to right) the date of inoculation, the date source pustules were counted, and the date secondary pustules were counted for Source Group 1 (lower axis) and Source Group 2 (upper axis), respectively.

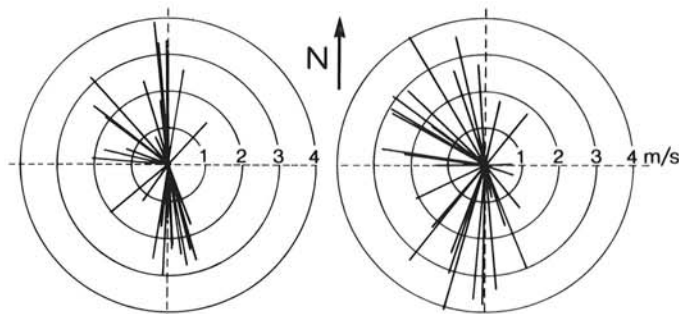


Fig. 5. Wind roses showing 2-hr average wind speeds (m/s) and directions (lines extend in the direction from which the wind is blowing) during 0800–2000 hr (when leaves were indicated to be dry based on the indications of the leaf wetness sensors) for days after planting 29–33 (left) and 34–38 (right). These time periods were judged the most likely for dispersal of the spores which resulted in the pustules counted on uninoculated plants for Source Group 1 and 2, respectively.

a plant, we expect that the deposition would more nearly resemble the predictions of equation 8a.

Disease development and distribution of pustules. Inoculations were made on days 20 and 25, first symptoms (raised whitish bumps) were observed on days 27 and 32, first open pustules on inoculated leaves were observed on days 31 and 35, and first open pustules on uninoculated leaves were observed on days 41 and 46, for Source Groups 1 and 2, respectively. The average latent period for the pathogen was estimated to be about 10.5 days, in reasonable agreement with that found elsewhere (15). The angular distribution of pustules on plants around sources generally reflected the patterns of wind direction (Fig. 5) during the window of time when the spores which resulted in the counted pustules were dispersed. For both source groups, there were about twice as many pustules to the east than to the west of the source (Fig. 6, open triangles). This reflected the fact that the wind was rarely from the east (Fig. 5).

The decrease in the number of pustules with distance from a source was described reasonably well by equation 10 for all experiments (Table 3). The numbers of pustules on individual plants is shown for Source 4 to illustrate the scatter in the data

(Figs. 7 and 8). These data were fitted reasonably well over the entire range by equation 10 with $L^2 = 148 \text{ cm}^2$, obtained using the average plant dimensions, i.e., $d = 20 \text{ cm}$, $W = 33 \text{ cm}$, and $H = 21 \text{ cm}$.

The model also described the shape of the decrease with distance of the average number of pustules, obtained by averaging over plants sampled with zones of distance (Fig. 6). Because the foliage of a plant extends over a range of distance, there is considerable uncertainty in the horizontal location of plants. For example, the average location of the foliage on the source plant is located at about 10 cm from the origin. The data are plotted at the mean distance from the source plant that the stems of the sampled plants emerged from the ground. The horizontal I-bars indicate the uncertainty in the mean position of the leaf area around these points. We estimated this uncertainty to be the Pythagorean sum of the SEM of the stem positions and the half-width of the horizontal extent of the plants. The lines shown in Fig. 6 were calculated using equation 10 with the values of A made to agree with the average number of pustules on the inoculated plants (excluding the source leaves). The parameter A of equation 10 was significantly correlated ($r_1^2 = 0.80$) with the initial number of pustules P_i on inoculated leaves (cf Table 3).

DISCUSSION

The model that we used to arrive at equation 10 is simple, yet it includes the basic physics needed to describe spore dispersal and deposition near a source. Its one adjustable parameter, A , depends on the number of spores released by the source. Our model also fits the data for bean rust presented by Mundt and Leonard (23). They used nonlinear regression to evaluate the three parameters in the equation $Y = a(x + c)^{-b}$ and made the suggestion that c of their equation may be related to the size of the source plant (23). Our analysis supports their suggestion. Our equation 10 gives $A = 3423.6$ and $L = 18.2 \text{ cm}$ ($r_1^2 = 0.98$ in the non-transformed space) and $A = 1264.4$ and $L = 21.7 \text{ cm}$ ($r_1^2 = 0.92$) for the data shown in Mundt and Leonard's Figures 3c and 3d, respectively.

It may be possible to obtain slightly better fits to the data by estimating all parameters using nonlinear regression. However, because the parameters obtained in this way may be interrelated, their interpretation is not always straightforward. For example, the data from our source 4 (Figs. 7 and 8) were fitted using Mundt and Leonard's equation (23) given above, and the resulting parameters were $a = 1.103 \times 10^6$, $b = 2.405$, and $c = 21.58 \text{ cm}$ ($r_1^2 = 0.973$ in the nontransformed space). The effective power,

TABLE 3. Values of the average number of pustules/leaf, P_i , the parameter A (\pm the standard error) of equation 10 obtained by regression, and the coefficient of determination, r_1^2 , of the fitted equation, for the 12 source regions where the initial spread of bean rust from single inoculated leaves was measured

Source	P_i^a	P_i^b	Plants ^c (no.)	Leaves ^c (no.)	A^d	r_1^2
1	1,119	38.3	98	853	418 \pm 44	0.78
2	1,432	37.1	91	919	474 \pm 45	0.82
3	288	31.5	84	974	399 \pm 33	0.87
4	457	43.5	91	846	543 \pm 30	0.94
5	1,206	45.6	72	720	875 \pm 67	0.91
6	328	10.0	94	1,100	99 \pm 11	0.78
7	541	15.0	88	933	125 \pm 12	0.82
8	166	12.0	91	974	55 \pm 9	0.84
9	85	10.7	72	677	50 \pm 7	0.75
10	383	25.8	83	872	235 \pm 24	0.83
11	198	16.3	86	867	140 \pm 13	0.85
12	219	18.6	87	1,079	139 \pm 16	0.77

^a Initial number of pustules on inoculated leaves.

^b Total number of pustules counted on all plants divided by the total number of leaves.

^c Total number of plants and leaves on which pustules were counted.

^d L^2 was set equal to 148 cm² for sources 1-5 and 263 cm² for sources 7-12.

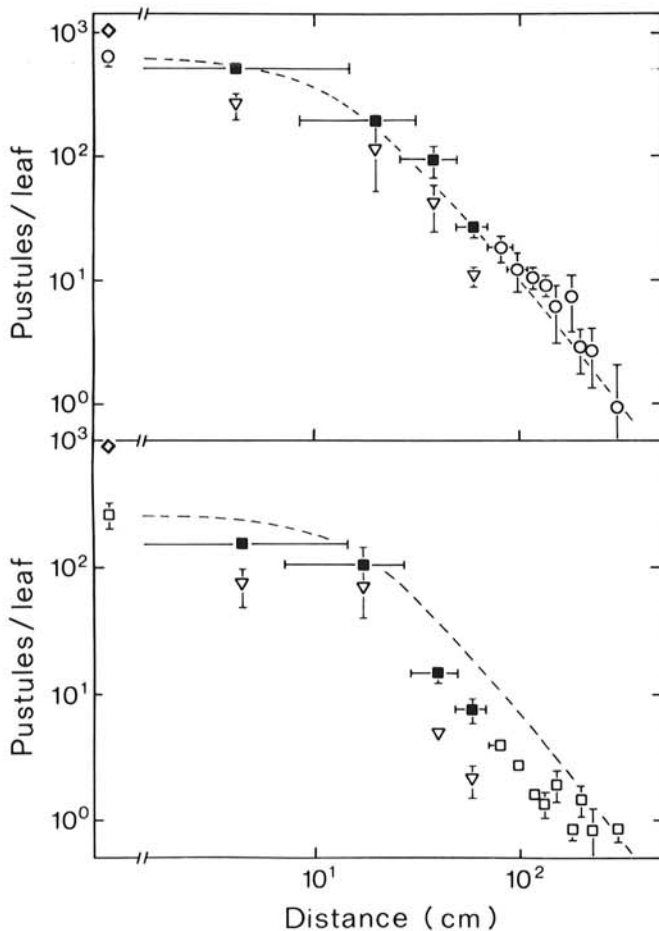


Fig. 6. Average number of new pustules per leaf versus distance from the inoculated plant for Source Group 1 (open circles, top) and Source Group 2 (open squares, bottom). Plotted are the total number of pustules divided by the total number of leaves in 20-cm annular rings around the source (with the exception of the first point where plants in a 10-cm radius circle centered at the origin were grouped). Also shown is the average number of pustules on plants in the source row to the east (filled squares) and west (open inverted triangles) of the inoculated plant. The vertical I-bars indicate standard errors of P_i , and the horizontal I-bars indicate the estimated uncertainty in the location of the corresponding leaf area. The dashed lines were calculated using equation 10 with $A = 593$ and $L^2 = 148 \text{ cm}^2$ (top) and $A = 264$ and $L^2 = 263 \text{ cm}^2$ (bottom), where the values of A were arbitrarily set equal to the mean number of pustules on the source plants (sans source leaves).

b_{eff} , of the above function changes with x and is the slope of the function on a log-log plot given by:

$$b_{\text{eff}} = [d \log(D)/d \log(x)] = b/(1 + c/x). \quad (11)$$

Therefore, at the mean sampled distance ($x = 100$ cm) the effective value of the exponent in the power law b_{eff} was 1.98, in reasonable agreement with our chosen value of 2. Similar regressions were performed for all of our sources. The fitted values of b ranged from 1.7 to 4.3; however, b_{eff} ranged only from 1.5 to 2.7 in reasonable agreement with $b = 2$ which we expect from geometrical considerations. Then, since we have shown how the required length scale parameter can be related explicitly to plant size, there remains only one scaling parameter to fit.

In arriving at equation 10, we assumed that the loss of spores from the air due to deposition has a relatively small effect on the overall pattern of deposition close to a source. The relative importance of spore deposition and turbulent diffusion in determining deposition patterns changes with distance from the source. It depends on how rapidly a plume of spores expands in the vertical direction and on the efficiency of spore deposition (1,5). By and large, the leaf area density of most crop canopies is relatively small and, excluding periods of calm, v_s/u_* is also small, where u_* is the friction velocity (31). The form of equation 10 hinges directly on our assumption that, close to a source, spore trajectories are essentially straight lines emanating from the source. In this case, deposition can be accounted for by multiplying equation 10 by $\exp(-Bs)$ (1), where B is defined by equation 1, so that:

$$P_p = \exp(-Bs) AN_1 (1 + s^2/L^2)^{-1}. \quad (12a)$$

In reality, of course, spores do not continue to travel in straight lines, and some of the spores which have left the canopy will return to the canopy and be deposited at some distance downwind. We used Chamberlain's (7) source depletion model to estimate the error in neglecting this effect. With Chamberlain's assumption that spores are well mixed vertically across the plume, it can be shown by analogy to the cylindrically symmetric case presented by Ferrandino (9) that equation 12a can be replaced by:

$$P_p = AN_1 (1 + s^2/L^2)^{-(1+f)}, \quad (12b)$$

where $f = LAI \cdot v_s / (2 \cdot U) = B \cdot H / 2$. For reasonable values of LAI, v_s and U , f is about 0.05–0.025. Thus, the power law is changed little by deposition, confirming that equation 10 is a reasonable approximation.

The number of secondary pustules on the inoculated leaves themselves could only be determined in five of twelve experiments; in the others, the inoculated leaves had abscised and could not be counted reliably. In those cases where we could determine autoinfection on the source leaf, as expected, the numbers of new pustules were considerably higher than on the rest of the source plant. We have treated the source leaves differently from the others by plotting them as separate points in Figs. 6 and 8.

The two parameters, A and L , of our model (equation 10) can be interpreted biologically. The scale factor A does not effect the shape of the disease gradient; it simply incorporates our ignorance about the exact number of pustules that will be produced on plants from a given number of pustules on a source leaf. The value of A depends on the number of spores released per pustule, on the efficiency of their deposition on plants, and on their infection efficiency, i.e., the number of infections per deposited spore. It is not presently possible to completely specify these factors under field conditions and, thus, A must be determined experimentally. The L effects the shape of our model equation and determines the location of the point of inflection. This point of inflection in the curve for deposition versus distance is a characteristic difference between the model presented here and the modification due to Mundt and Leonard (23). Physically, L is related to the mean pathlength for spore deposition through a plant.

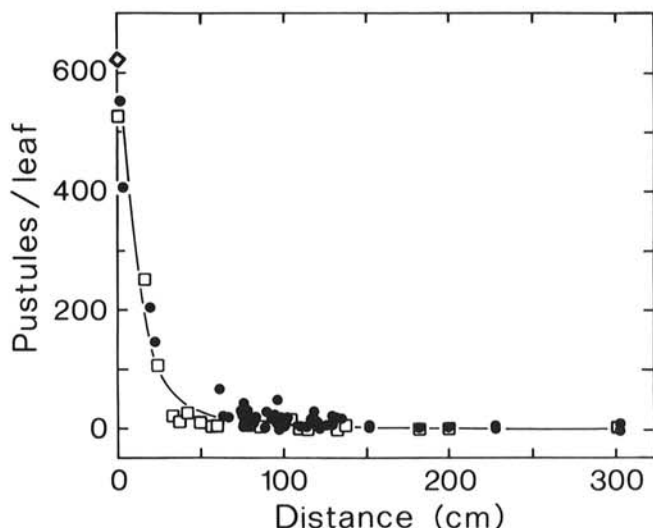


Fig. 7. The number of new pustules per leaf on individual plants harvested at various distances from the inoculated leaf for source 4 (Table 3). The diamond represents the source plant (sans source leaf). The squares represent plants located in the western quadrant. The line is equation 10 with $A = 543$, $L^2 = 148 \text{ cm}^2$, $r^2 = 0.94$, $df = 90$.

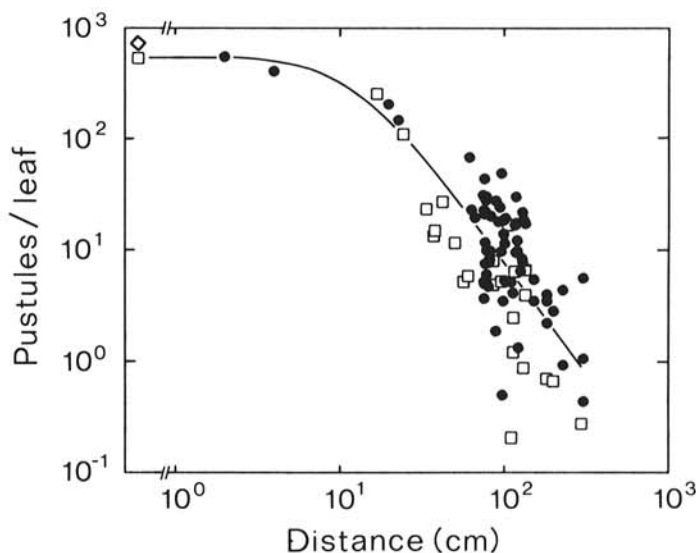


Fig. 8. Same as Fig. 7, except log-log coordinates have been used to better illustrate the ledge near the origin and the slope at distance.

In conclusion, we have presented a simple geometrically based modification of the inverse power law that adequately describes the primary spread of bean rust within 3 m of inoculated leaves. The shape of the predicted deposition is totally determined by one length scale which is directly related to the spatial dimensions of a sampled plant. The only adjustable parameter in the model is related to the number of spores released at the source. Future improvements in our model will require a better understanding of the local patterns of air movement near the leaf surface during liberation of urediniospores by wind which cannot be described by the simple radially diverging flow field we have used in the model.

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